UNIVERSITY OF CALIFORNIA

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# Miocene ungulates from Laguna del Laja, Chile, and an assessment of the Laguna del Laja faunas.

A dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy in Earth Science

by

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The dissertation of Daniel Alexander Luna is approved.

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This dissertation represents a culmination of many things I've learned, and though much of that knowledge is related to South American paleontology, there have also been other important lessons along the way. In my experience, the most valuable lessons often involve exceptional teachers. Indeed, I have received substantial support and guidance throughout this undertaking. I owe a debt of gratitude to many individuals and institutions, but the greatest share of my thanks goes to my advisor, Andy Wyss. Not only has Andy been an excellent mentor, introducing me to several different phases of paleontological discovery, but he has also become a friend and role model. His patience, kindness, and encouragement have been constant, and these virtues serve as inspiring examples to follow in my own life. I think I'd need a sixth chapter in this dissertation to adequately convey the full range of my respect and appreciation for Andy, but I know that he would humbly deflect such praise, and that he values concision.

Over the years, I've learned that, like any vocation, research can be enriched immeasurably by the people you're working with. I've been extremely fortunate to be part of such an excellent team, including Andy, John Flynn, and Darin Croft. I'm truly humbled by what they've been able to accomplish together, and their support has given this phase of my life significance far beyond the academic.

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March 2015

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Luna, D., Flynn, J., Croft, D., Wyss, A. 2013. Taxonomy, Biogeography, and Phylogeny of Miocene Endemic South American Ungulates (Mammalia) from the Laguna del Laja Region, Andean Main Range, Central Chile. Journal of Vertebrate Paleontology, Program and Abstracts, 2013, 166.

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# ABSTRACT

Miocene ungulates from Laguna del Laja, Chile,
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by

Daniel Alexander Luna

The unique history of mammals in South America has long provided significant evolutionary and geological insights, but the continent's fossil record is strongly biased toward the lowlands of Argentine Patagonia. Recent collecting efforts in the Andean Main Range of Chile, near Laguna del Laja (LdL) (~37.5º S, 71º W), have yielded a stratigraphically superposed series of early to late Miocene fossil mammal assemblages, shedding light on the poorly known extra-Patagonian history of South American Neogene mammals. Several hundred specimens have been recovered from the Cura-Mallín and overlying Trapa-Trapa formations at LdL. Nearly all of these fossils were collected from a well-described stratigraphic sequence that includes 17 high precision $^{40}Ar/^{39}Ar$ ages. This robust temporal framework encompasses fossiliferous horizons spanning ~20-9 Ma. Herein I provide a detailed account of the ungulates from the Cura-Mallín Formation at LdL; these range in age from ~20-15 Ma (early to middle Miocene). Dentitions referred to *Protypotherium praerutilum*, a well-known but inadequately diagnosed species, motivated a long overdue (but preliminary) taxonomic revision. Occurrences of *Protypotherium*, *Colpodon*, and *Astrapothericulus*, together with radioisotopic ages, indicate that faunas

spanning the Colhuehuapian and Santacrucian South American Land Mammal "Ages" (SALMAs) occur in direct stratigraphic superposition at LdL. These deposits have also yielded five new genera of typotherians (Notoungulata); this high level of endemism has also been noted among rodent faunas from LdL. The five new taxa described in this study are included in rigorous phylogenetic analyses of Interatheriinae and Hegetotheriidae (Typotheria, Notoungulata), providing new hypotheses of morphological evolution within these clades, and documenting independent yet apparently simultaneous radiations of interatheres and hegetotheres with ever-growing (hypselodont) dentitions. A significant majority of fossils from LdL are small-bodied taxa (e.g., rodents and typotherian notoungualtes) represented by dental and cranial elements. This size distribution is unusual compared to other well-known early Miocene faunas, and may reflect differential transport of skeletal elements in lahar-associated depositional settings. The high level of endemism across multiple SALMAs at LdL is also striking, particularly considering the geographic proximity of faunas from LdL with roughly coeval counterparts in neighboring regions of Argentina. This provinciality of the Andean faunas, relative to Argentine assemblages, likely reflects sampling of a regionally distinct and isolated paleoenvironment.

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# Chapter 1. Introduction

## Overview of Cenozoic mammals in South America

South America was an island continent for most of the Cenozoic, providing a unique stage for the ever inventive pageant of evolutionary theater. With the breakup of Pangea, South America rifted from North America in the Late Jurassic, and from Africa in the Early Cretaceous (Wilf *et al*., 2013). At the end of the Cretaceous, the tectonic and biogeographic record suggests a series of intermittent connections between North and South America (Case *et al*., 2005; Pascual, 2006), through which the first therian mammals arrived in South America by the early Paleocene (Pascual and Ortiz-Jaureguizar, 1990a; Muizon and Brito, 1993; Ortiz-Jaureguizar, 1996; Goin *et al*., 2006; Gelfo *et al*., 2009). This pathway for biotic dispersal appears to have closed sometime in the Paleocene (Case *et al*., 2005), and the prolonged geographic isolation of South American therian mammals resulted in a unique and fascinating evolutionary history.

Simpson (1948, 1950, 1967, 1980) identified three major episodes in South American mammal evolution during the Cenozoic – the so-called "Three Faunal Strata" – introducing a historical framework that is still broadly useful today (e.g., Patterson and Pascual, 1968; Marshall, 1988; Pascual and Ortiz-Jaureguizar, 1990b; Flynn and Wyss, 1998; Flynn et al., 2003, 2012; Croft *et al*., 2008; Goin *et al*., 2012) (fig. 1.1). During the "First Faunal Stratum" the South American mammal record is dominated by an "original stock" including only three major groups – marsupials (pouched forms), xenarthrans (extant representatives include sloths, armadillos, and anteaters), and

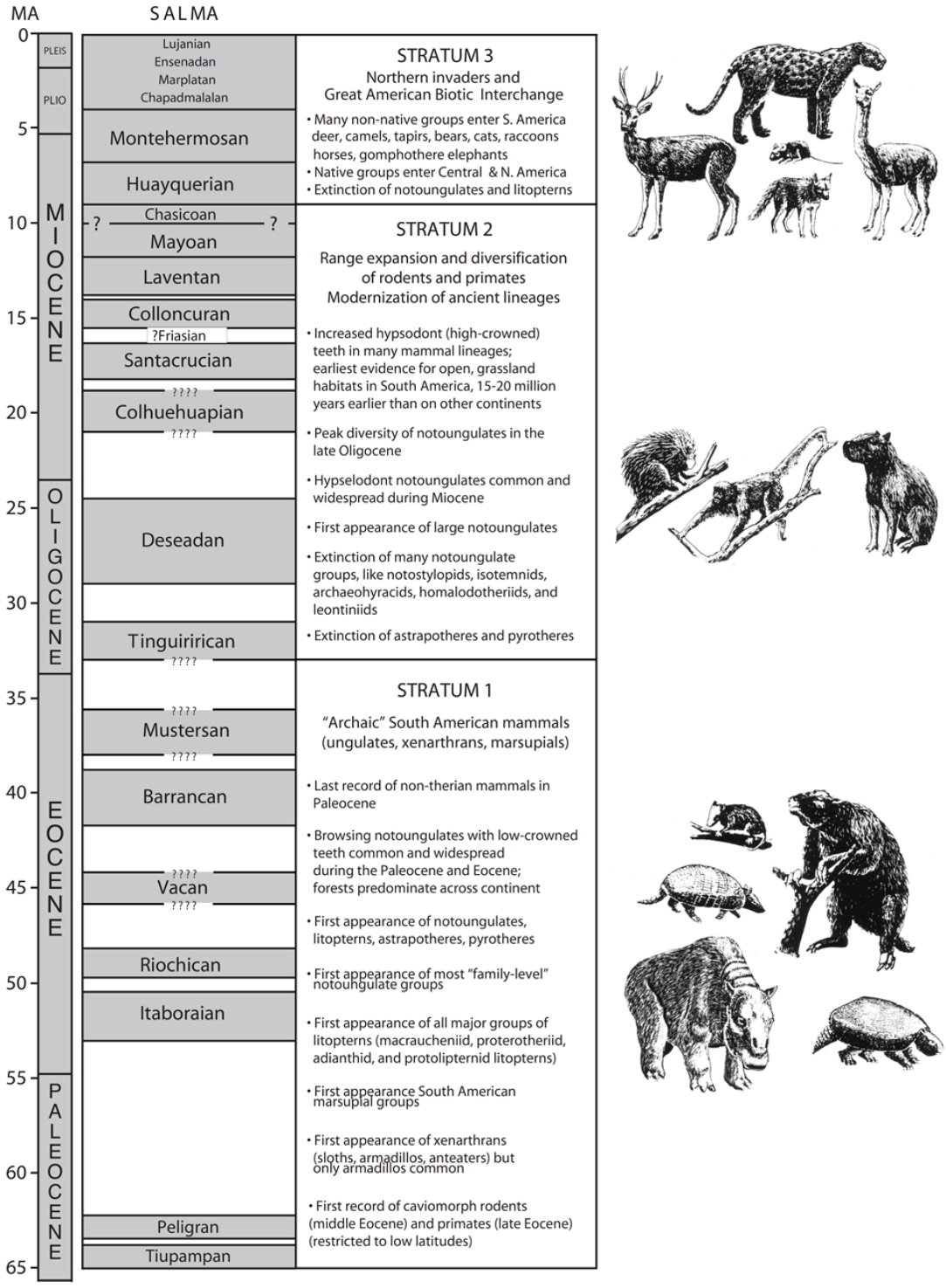



FIGURE 1.1. South American Land Mammal "Ages" (SALMAs) and the "Three Faunal Strata." Modified from Flynn *et al*. (2012). The SALMA biochronology is calibrated to the Cenozoic timescale following Flynn *et al*., 2012, with Paleogene SALMA ages modified according to Woodburne *et al*., 2014. Major features of "Faunal Strata" are listed (following Flynn *et al*., 2012), with rodent and primate distributions updated in light of recent discoveries (Antoine *et al*., 2012; Bond *et al*., 2015). The description of each "Faunal Stratum" is not calibrated to the timescale, and illustrated animals (right) represent groups typical of each stratum rather than their complete temporal ranges

several extinct groups of native ungulates (hoofed herbivores). The hegemony of this "original stock" came to an end after the immigration of rodents and primates; a growing consensus suggests that these latter two groups reached South America via a trans-Atlantic dispersal from Africa (Hoffstetter, 1972; Lavocat, 1976; Wyss *et al.*, 1993; Flynn *et al.*, 1995; Huchon, 2001; Opazo *et al.*, 2006; Poux *et al.*, 2008; Bandoni de Oliveira *et al.*, 2009; Antoine *et al.*, 2012; Bond *et al.*, 2015). Recently described fossils from two different localities in Peru indicate that rodents had arrived in South America by the middle Eocene (~41 Ma) (Antoine *et al.*, 2012), followed by primates in the late Eocene (Bond *et al.*, 2015).

The beginning of the "Second Faunal Stratum" is roughly coincident with the rapid greenhouse-icehouse transition that occurred near the Eocene-Oligocene boundary (~34 Ma) (Miller *et al.*, 1987; Zachos e*t al.*, 2001), likely associated with the opening of the Drake Passage (disconnecting South America and Antarctica) and the establishment of the Antarctic Circumpolar Current (Kennett, 1977; Livermore *et al.*, 2004). Spanning the early Oligocene to late Miocene, the "Second Faunal Stratum" is characterized by the range expansion and diversification of rodents and primates (see MacFadden, 1990; Wyss *et al.*, 1993; Fleagle *et al.*, 1997; Kay *et al.*, 1998; Antoine *et al.*, 2012; Bertrand *et al.*, 2012), and significant faunal turnover and modernization within the "original stock" of marsupials, xenarthrans, and native ungulates (e.g., Goin *et al.*, 2010; Flynn *et al.*, 2003; Croft *et al.*, 2008).

The "Third Faunal Stratum" commenced ~6 million years ago (Webb, 1985) (but possibly as early as ~9.5 Ma; see Campbell *et al.*, 2000, 2010), as North and South America became increasingly connected via an evolving volcanic island arc, providing new pathways

for dispersal, and eventually forming (~3 million years ago) the Central American land bridge (Coates *et al*., 2004; Bartoli *et al*., 2005). The resulting "Great American Biotic Interchange" – a remarkable natural experiment in evolution – is well documented in the fossil records of both continents (e.g., Marshall *et al*., 1982; Stehli and Webb, 1985; Marshall, 1988; Woodburne *et al*., 2006; Morgan, 2008; Woodburne, 2010).

## South American Land Mammals "Ages"

Along with the major faunal shifts of the "Three Faunal Strata," many smaller-scale changes are also observed within lineages of South American mammals – including the first and last appearances of taxa at various taxonomic levels, shifting faunal associations, and the development of derived morphological features. Accordingly, South American paleo-mammal assemblages have been used for biostratigraphic correlation for over a century (e.g., Hatcher, 1897; Tournouër, 1903; Ameghino, 1906; Gaudry, 1906), with new fossil discoveries being incorporated into the framework of these initial observations. This continuously growing body of knowledge has been expanded, debated, modified, and formalized by many researchers (e.g., Loomis, 1914; Kraglievich, 1930; Frenguelli, 1930; Simpson, 1933, 1940; Paula Cuoto, 1952, 1978; Patterson and Pascual, 1968; Marshall *et al*., 1977, 1983; Marshall, 1982; Muizon, 1991; Bonaparte *et al*., 1993; Cione and Tonni, 1995; Flynn and Swisher, 1995; Madden *et al*., 1997a; Flynn *et al*., 2003; Cerdeño *et al*., 2008; Bond and Deschamps, 2010; Kramarz *et al*., 2010; Woodburne *et al*., 2014). Paleontologists currently recognize over 20 South American Land Mammal "Ages" (SALMAs) (fig. 1.1), each defined by a characteristic assemblage of coexisting mammals.

The relative ages of these SALMAs are generally well established, but constraining these intervals with precise "absolute" ages remains an active area of research (e.g., Flynn and Swisher, 1995 [and references therein]; Madden *et al*., 1997a; Flynn *et al*., 1997, 2003; Wertheim, 2007; Gelfo *et al*., 2009, Re *et al*., 2010; Perkins *et al*., 2012; Fleagle *et al*., 2012; Dunn *et al*., 2013; Woodburne *et al*., 2014). The regional applicability of the SALMA sequence also remains an open question, especially as each SALMA originally corresponds to (and derives its name from) a particular "type" locality and its associated fauna (e.g., the late early Miocene Santacrucian SALMA was initially recognized in reference to fossils recovered near Puerto Santa Cruz, in Argentine Patagonia). Fossil collections from geographically widespread areas have improved our knowledge of the regional diversity of South American paleo-mammal communities, but has also sometimes made it difficult to correlate geographically distinct faunal assemblages (e.g., Cione and Tonni, 1995; Madden et al., 1997a; Flynn *et al*., 2002a; Croft, 2007; Kramarz *et al*., 2010). While similar challenges are encountered in establishing "land mammal ages" on other continents (see Evernden *et al*., 1964; Savage and Russell, 1983; Woodburne, 1987; Lindsay *et al*., 1989; Walsh, 1998), this problem is magnified in South America, since much of the SALMA sequence was established on the basis of faunas from Argentine Patagonia (reviewed in Patterson and Pascual, 1968; Marshall *et al*., 1983; Pascual and Ortiz-Jaureguizar, 1990b), while the continent spans approximately 70° of latitude (from ~12°N to ~56°S) with 70% of its land area occurring above the Tropic of Capricorn (Madden *et al*., 1997a). Despite these limitations, researchers employ robust biostratigraphical, morphological, geochronological, and/or phylogenetic data to correlate geographically widespread faunas (e.g., Marshall, 1982; Marshall and Sempere, 1991; Cione and Tonni, 1995; MacFadden *et al*., 1985; Flynn and Swisher, 1995; Madden *et al*., 1997a; Flynn *et al*., 2002a, 2003; Croft, 2007; Wertheim,

2007; Gelfo *et al*., 2009; Tonni *et al*., 2009; Anotoine *et al*., 2012; Bostelmann, 2013); the ever-growing fossil record renders such efforts a continual work in progress.

## On the abundance and influence of fossils from Argentine Patagonia

Fossils from Argentina are pivotal to our understanding of mammal evolution in South America. The first formal classification of a South American fossil is attributed to the illustrious French naturalist George Cuvier (1796), who described *Megatherium americanum*, a giant sloth, based on a specimen recovered from along the banks of Río Lujuán, Buenos Aires Province. The particularly rich fossil beds of Argentine Patagonia have tremendously influenced the development of paleontology on the continent. The first fossils described from these high latitudes were collected from along the banks of Río Gallegos in 1845 by Captain Bartholomew Sulivan (Brinkman, 2003). Sulivan sent these remains to his former shipmate aboard the HMS *Beagle*, Charles Darwin, who would in turn pass them on to the famed anatomist Richard Owen (Brinkman, 2003). Examining these fossils, Owen (1846) described a new species, *Nesodon imbricatus*, now recognized as a toxodontian notoungulate (see below), representing the first Miocene-aged vertebrate described from South America.

These initial discoveries, which auspiciously involved the preeminent luminaries of natural history of the 18$^{th}$ and 19$^{th}$ century, can be considered early heralds of a Patagonian golden age of paleontology that would commence at the approach of the 20$^{th}$ century. The beginning of this phase coincides, in large part, with the enormously productive careers of two Argentine brothers, Florentino and Carlos Ameghino. Florentino Ameghino, who

eventually became the first Argentinian director of the Museo Argentino de Ciencias Naturales Bernardino Rivadavia, in Buenos Aires, described hundreds of new species, with much of his voluminous work focusing on Patagonian fossil mammals (e.g., F. Ameghino, 1887, 1889, 1894, 1895, 1897, 1902, 1906); many of the thousands of specimens Florentino studied, described, and curated were collected by his brother Carlos (e.g., C. Ameghino, 1890, 1891). Lured by the rich fossil beds of Patagonia, and, in some cases, encouraged by the prolific output of the Ameghino brothers, researchers from Argentina, the United States, and Europe mounted numerous expeditions, some of immense scale and duration, to Argentina's southern latitudes, yielding an enormous trove of fossils in the late 19$^{th}$ and early 20$^{th}$ centuries (Roth, 1898; Hatcher, 1903; Tournouër, 1903; Gaudry, 1904; Sinclair, 1909; Loomis, 1914; Rovereto, 1914; Riggs, 1928). Consequently, the Patagonian fossil record has long dominated South American paleontology, and much of our knowledge of mammal evolution in South America still reflects this Patagonian bias (summarized by Marshall et al., 1983; Pascual and Jaureguizar, 1990b; Pascual et al., 1996).

## Paleo-mammal faunas from the Andean Cordillera

In recent decades, efforts to collect fossils outside of Argentina have expanded our knowledge of the diversity and biogeography of South America's ancient mammals. Scores of new specimens, and many new taxa, have been reported from Bolivia, Brazil, Chile, Colombia, Ecuador, Peru, and Uruguay (see concise summary and references in Croft, 2007). The Andean Cordillera has provided especially fertile ground for new fossil discoveries. The Andes, spanning ~7000 km from north to south, are the longest mountain

chain on Earth. They are also uniquely long-lived, with subduction-related orogenesis and magmatism along the western margin of South America dating back to at least the early Jurassic (Harmon and Rapela, 1991; Oncken *et al*., 2006). This ancient and ever-changing volcanic arc has long provided unique habitats for the cordillera's inhabitants; today, several aspects of these unique settings are providing valuable paleontological insights. In addition to extending the spatial sampling of South America's paleo-mammals, Andean sedimentary sequences and their associated fossils have revealed unexpected depositional and preservational environments, enabled unique paleoenvironmental inferences, provided abundant opportunties for geochronologic calibration, and helped fill in temporal gaps in the Cenozoic fossil record.

Several paleontologically significant Andean localities, ranging geographically from Colombia to Southern Chile, and temporally from early Paleocene to middle Miocene, are shown in figure 1.2. Some of the insights gained from these cordilleran fossils are highlighted below. Faunas from Laguna del Laja contribute to this growing Andean archive of mammal evolution in South America.

The fauna from Tiupampa, which led to the recognition of the Tiupampan SALMA, represents the oldest well-studied assemblage of Cenozoic fossil mammals in South America (Muizon, 1991, 1998; Muizon and Brito, 1993; Marshall *et al*., 1997; Sempere *et al*., 1997; Muizon and Cifelli, 2000, 2001; Gelfo *et al*., 2009). Collectively, these studies document an early phase of therian mammal dispersal and radiation on the continent, with a marked diversity of marsupials, but an absence of xenarthrans and many ungulate groups that characterize later faunas. Only therian mammals are recorded at Tiupampa, but non-therian gondwanatheres are known from a later fauna in Argentine Patagonia (Peligran SALMA)


FIGURE 1.2. Map of South America indicating the Andean fossil localities discussed in the text. The SALMAs associated with these faunas are highlighted in bold type (see text for references). The fauna from Las Leñas has yet to be correlated to a SALMA, preliminary assessments, combined with a single $^{40}Ar/^{39}Ar$ date of 20.09 ± 0.27 Ma (Flynn *et al*., 1995), suggest an early Miocene age. Most fossils treated in the present study were recovered from the Laguna del Laja region (green square); one specimen from Las Leñas is also described.

(Pascual *et al*., 1992; Bonaparte *et al*., 1993), suggesting that non-therian mammals persisted at higher latitudes as relicts of a wider Mesozoic distribution (Gelfo *et al*., 2009).

Oligoene and Miocene-aged fossils are also well represented in the Bolivian Andes, including the middle Miocene fauna at Quebrada Honda (Hoffstetter, 1977; MacFadden and Wolff, 1981; Frailey 1987, 1988; MacFadden *et al*., 1990; Marshall and Sempere, 1991; Goin *et al*., 2003; Forasiepi *et al*., 2006; Croft and Anaya, 2006; Croft, 2007; Engleman and Croft, 2014) and the late Oligocene fauna at Salla (Hoffstetter, 1968; Villaroel and Marshall, 1982; Wolff, 1984; MacFadden *et al*., 1985; Engelmann, 1987; Vucetich, 1991; Sanchez-Villagra *et al*., 1997; Shockey, 1997, 2005; Kay *et al*., 1998; Reguero and Cerdeño, 2005; Pujos and de Iuliis, 2007; Hitz *et al*., 2008; Shockey and Anaya, 2008; Billet *et al*., 2009). The Salla fauna, corresponding to the Deseadan SALMA (late Oligocene), includes the earliest mid-latitude record of primates in South America (Kay *et al*., 1998), while the Quebrada Honda fauna has been referred to the Laventan SALMA (middle Miocene). Many new taxa have been described from both of these Bolivian localities, suggesting that large-scale faunal provinciality in South America was well-established by the late Oligocene (Flynn *et al*., 2012). It is especially striking, for example, that the Quebrada Honda fauna is more similar to earlier faunas from Patagonia (Colloncuran SALMA) than to the coeval La Venta fauna of Colombia (Croft, 2007).

The middle Miocene fauna from La Venta, Colombia, which led to the recognition of the Laventan SALMA, represents one of the richest vertebrate fossil records in all of South America. The earliest documented collecting efforts in La Venta date back to the 1920s (Ariste-Joseph and Nicéforo-María, 1923), and between the 1940s to the 1990s numerous institutions from Colombia, the United States, France, and Japan organized expeditions to the region (a summary of these expeditions and their associated publications is detailed in

Madden *et al*., 1997b). Highlighting the richness of these fossil beds, Madden *et al*. (1997b) report that, between 1985 and 1992, the Instituto Colombiano de Geología y Minería and Duke University collected and catalogued 3,272 specimens; a comprehensive volume describes these fossils and provides a summary of the La Venta fauna (Kay *et al*., 1997). As with the mid-latitude Bolivian faunas, the extent of endemism at La Venta indicates a high degree of provinciality in the middle Miocene. Of particular importance is the diversity of primates at La Venta: at least nine platyrrhini genera are recognized from these deposits; no other South America paleofauna records more than two (Fleagle et al., 1997; Croft, 2007).

Recent collecting efforts have yielded early Miocene faunas from the northernmost and southernmost Andes of Chile. Fossils from Chucal, in the northern Altiplano (Flynn *et al*., 2002a; Croft *et al*., 2004, 2007; Charrier *et al*., 2005), and Pampa Castillo, in Patagonia, are likely cotemporal (Santacrucian SALMA), yet these faunas show marked differences. The Patagonian Pampa Castillo fauna is taxonomically very similar to "type" Santacrucian faunas (recovered from Argentine Patagonia), but the Chucal fauna is notably characterized by: 1) a high degree of taxonomic novelty, an abundance of mesotheriid notoungulates (well-known in coeval and younger Bolivian localities, but absent in the middle Miocene La Venta fauna, and not recorded until the late Miocene in Patagonia); 2) an unexpectedly early occurrence of chinchilline rodents; and 3) the absence of interatheriid notoungulates (which are common in the late Oligocene through middle Miocene at both lower and higher latitudes) (Croft *et al*., 2004; Flynn *et al*., 2012). Recently reported from southern Chile, fossils from Sierra Baguales may represent a transitional Colhuehuapian/Santacrucian fauna (Bostelmann *et al*., 2013). Sedimentological inferences at Sierra Baguales and the marine-terrestrial record at Pampa Castillo both suggest that significant uplift of the southern Andes

commenced by ~18 Ma (Flynn *et al*., 2002b; Bostelmann *et al*., 2013), highlighting the types of geological insights that are often concomitant with paleontological investigations.

Several fossil localities are known from the Andes of central Chile, with faunas likely ranging in age from ?middle Eocene to early Miocene (summarized in Flynn *et al*., 2012; see fig. 4.3 therein). Of these, the most extensively studied is the fauna recovered from the upper Río Tinguiririca valley (~160 km south southeast of Santiago), which has helped fill in a large gap in the early Oligocene fossil record of South America, leading to the recognition of the Tinguiririca SALMA (Wyss *et al*., 1990, 1993, 1994; Flynn *et al*., 2003; Hitz *et al*., 2000, 2006; Croft *et al*., 2003a, 2008; Reguero *et al*., 2003a; Bertrand *et al*., 2012). The Tinguiririca fauna documents a major faunal transition (the beginning of Simpson's "Second Faunal Stratum"), including the last appearance of some "archaic" mammal groups, the first record of many lineages known from later SALMAs, and the first widespread occurrence of hypsodonty (high crowned dentition) among notoungulates. Paleoenvironmental analyses of these fossils suggest a moderately dry and relatively open habitat, and may indicate that grasslands became common in South America 10-15 million years earlier than on other continents (Croft, 2000, 2001; Flynn *et al*., 2003, 2012; but for alternate interpretations see Stromberg *et al*., 2013; Madden, 2014). Potentially correlative faunas with some taxonomic similarities have been recognized elsewhere in Chile and Argentina (Hitz *et al*., 2000; Flynn and Wyss, 2004; Flynn *et al*., 2003; Reguero *et al*., 2003a; Croft *et al*., 2008), but here again provinciality may limit the regional applicability of biochronologic correlation (Flynn *et al*., 2012). The fauna from Las Leñas, in the Andes of central Chile (~100 km south southeast of Santiago), has yet to be comprehensively studied, but one specimen has received considerable attention: the remarkably well-preserved cranium of *Chilecebus carrascoensis* represents one of the most complete fossil primate

skulls in South America, and its discovery provided key support for an African origin of New World anthropoids (Flynn *et al*., 1995). Herein I recognize a new species of notoungulate from Las Leñas (and from the Laguna del Laja region, ~240 km to the SSW) (Ch. 2).

## Laguna del Laja fossils: geographic, geological, and paleontological context

The region near Laguna del Laja (LdL) – approximately 500 km south of Santiago, in the Andes of central Chile (~37.5°S, 71°W) (fig. 1.3) – was reconnoitered for fossils during field seasons from 2001-2005. The lake itself formed when a sector collapse of Volcán Antuco (just south of the lake) dammed the Río Laja drainage ~10 ka before present (Thiele *et al*., 1998). LdL and its associated tributaries and outlets are bordered (and undoubtedly underlain) by thick sequences of volcaniclastic strata in a region with generally sparse vegetation cover, high topographic relief, and relatively easy access, providing a beautiful, rugged, and productive setting for geological and paleontological investigations (fig. 1.4).

Most fossils from the LdL region were recovered southeast of the lake (and Volcán Antuco), where thick sequences of the volcaniclastic Cura-Mallín Formation (CMF) and overlying Trapa-Trapa Formation (TTF) are exposed (several specimens were also recovered from the CMF a few kilometers north of LdL in 2004). Gonzáles and Vergara (1962) initially mapped (1:500,000 scale) and described the CMF, regarding these strata as Jurassic in age. Through a more detailed (1:250,000 scale) mapping effort, Niemeyer and Muñoz (1983) recognized the TTF as distinct from the underlying CMF. The CMF is composed primarily of volcaniclastic mudstones, sandstones, and conglomerates with interbedded tuffs

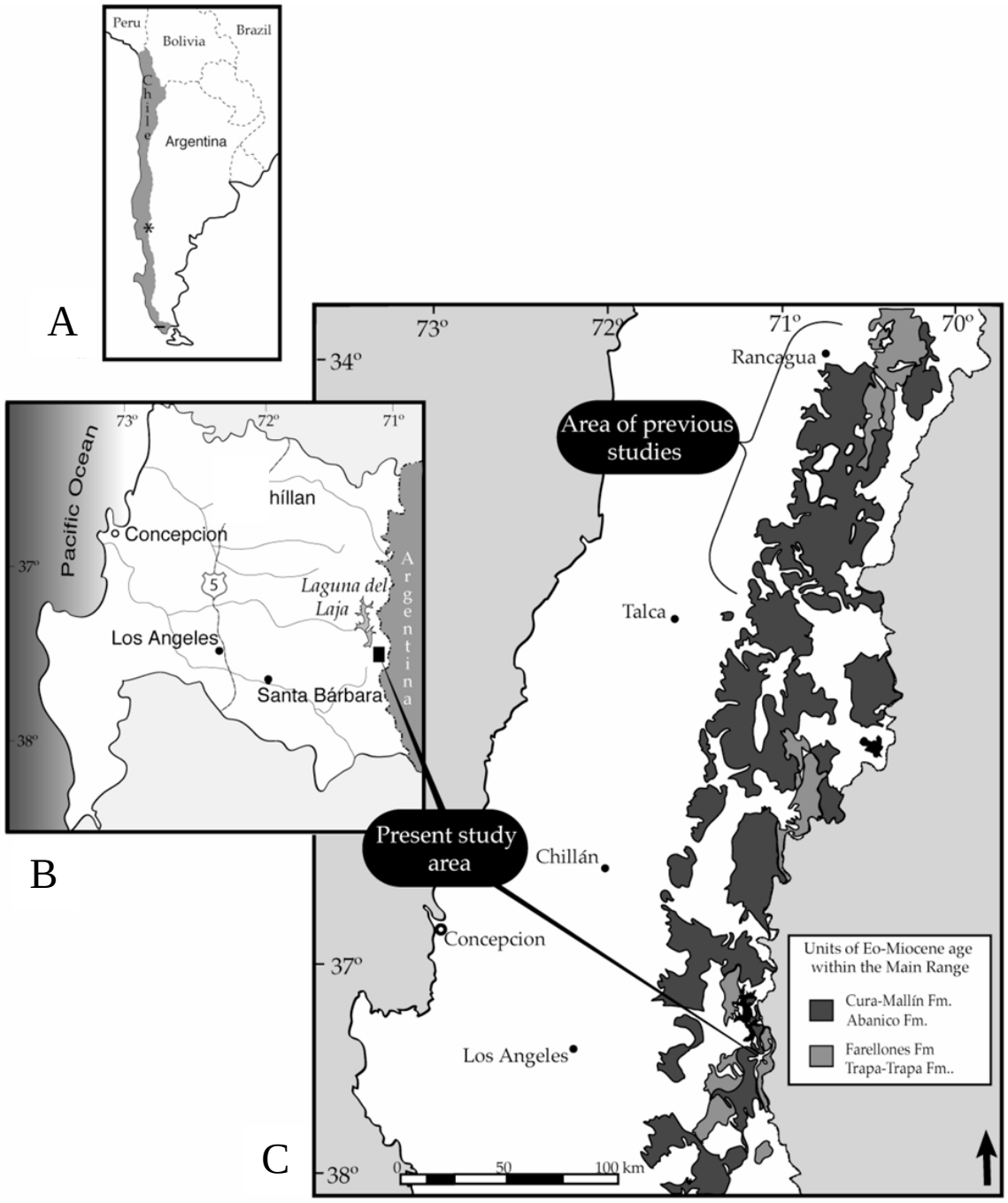



FIGURE 1.3. Map of the of the Laguna del Laja study area (from Wertheim, 2007). **A**: South America's "Southern Cone," with Laguna del Laja study region indicated by a star. **B**: Map of Bío Bío Province, Chile. Most fossils in this study were collected from a ~100 $km^2$ area (black rectangle) southeast of Laguna del Laja. **C**: Map of Central Chile showing the distribution of the Cura Mallín/Abanico and Trapa Trapa/Farellones formations. Laguna del Laja is colored black. "Area of previous studies" refers to localities in the Andes of central Chile that have yielded several ?Eocene to Miocene-aged mammal faunas, including those from Las Leñas and Tinguiririca (discussed in the text and shown in fig. 1.2).


A


B

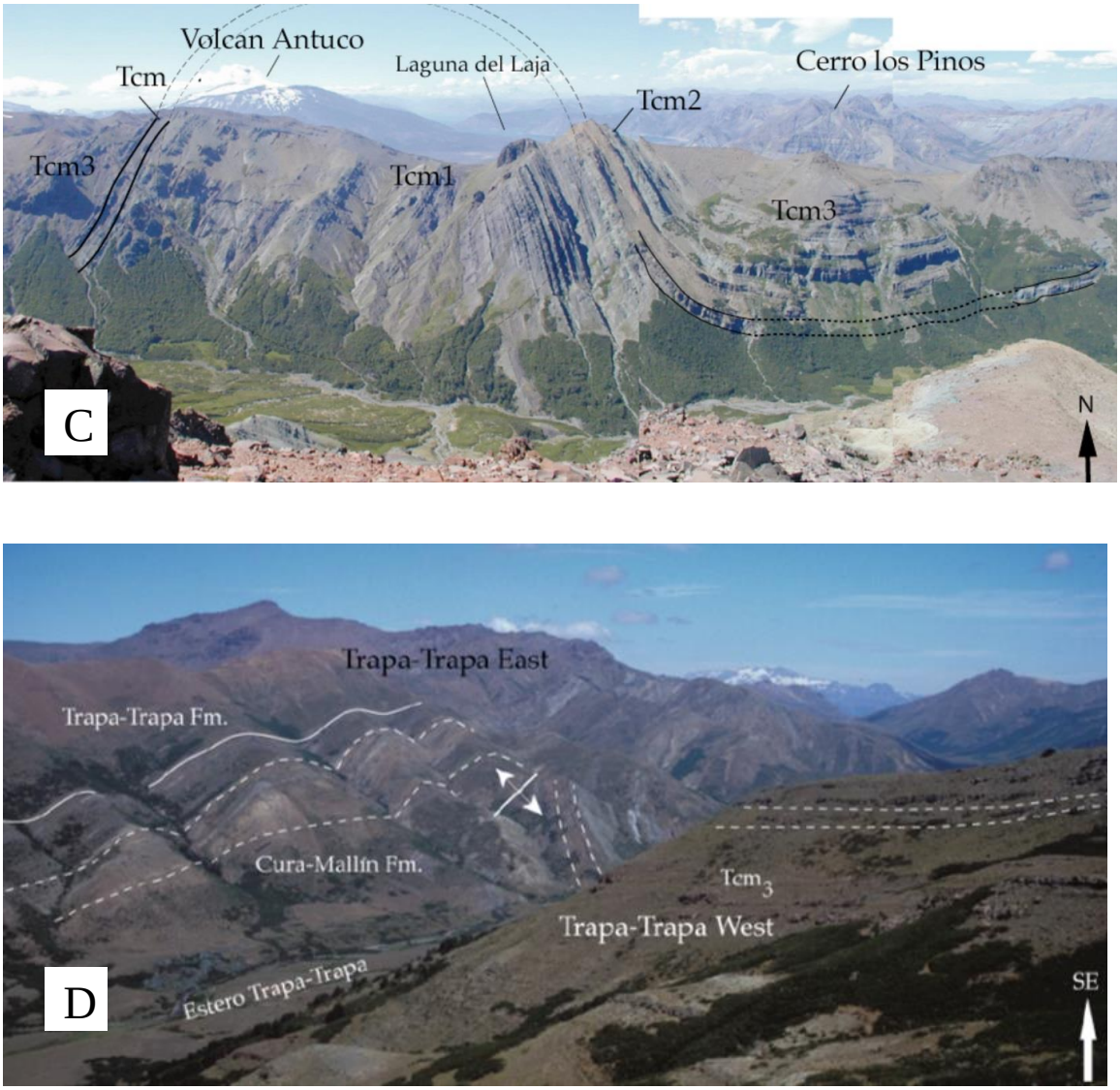



FIGURE 1.4. Photographs from the Laguna del Laja region, including some geological interpretations (refer to figs. 1.6 and 1.7 for an explanation of symbols, locality designations, and unit abbreviations/descriptions). **A**: View of Volcán Antuco (left) and Laguna del Laja (right) from Cerro Los Pinos (facing northwest) (from Herriot, 2006). **B**: View to the northeast of Cerro Los Pinos, displaying the beautiful and rugged terrain in the region (from Herriot, 2006). **C**: View of the north wall of Estero Campamento, taken from the south wall, highlighting kilometer-scale folds and landmarks in the background (from Wertheim, 2007). **D**: Estero Trapa Trapa East as seen from Estero Trapa Trapa West, providing a view of an anticline in the Cura Mallín Formation below its contact with the Trapa Trapa Formation (from Wertheim, 2007).

and ignimbrites, whereas the TTF includes numerous lava flows and coarser volcaniclastic breccias and conglomerates (Niemeyer and Muñoz, 1983; Suárez and Emparán, 1997; Herriott, 2006). Niemeyer and Muñoz (1983) proposed an Eocene to middle Miocene age for the CMF, based on one $^{40}K$-$^{40}Ar$ age and inconclusive non-vertebrate paleontological data. In subsequent years, several studies sought to constrain the age of the CMF and TTF, but contradictory and ambiguous results were left unresolved (see summary in Herriott, 2006, pgs. 19-22, and fig. 3.1 therein). Recent geological studies southeast of LdL have helped to clarify the lithostratigraphic relationships, ages, and depositional settings of the CMF and TTF in this region (Herriott, 2006; Flynn *et al*., 2008).

The CMF is exposed in the Andes between ~36°S and ~39°S, and the TTF conformably overlies the CMF between ~36°S and ~37.5°S (Herriott, 2006). Charrier *et al*. (2002) proposed that the CMF and TTF may be lateral equivalents of the Abanico (~33°-36°S) and Farrellones (~33°-35S) formations, respectively (fig. 1.3c). The Abanico Formation (Late Cretaceous to middle Miocene [Mosolf, 2013]) records several paleo-mammal faunas, possibly ranging in age from middle Eocene to early Miocene (summarized in Flynn *et al*., 2012; see fig. 4.3 therein), including the well-studied early Oligocene Tinguiririca fauna that led to the recognition of the Tinguiririan SALMA (Wyss *et al*., 1990, 1993, 1994; Flynn *et al*., 2003; Hitz *et al*., 2000, 2006; Croft *et al*., 2008). As detailed in Chapter 2, a pair of conspecific dentitions recovered ~240 km apart, one from the Abanico formation near Las Leñas and the other from the CMF north of LdL, highlight the temporal and faunal continuity of these formations.

Between ~37°S and ~39°S, the CMF was likely deposited in two half-grabens (northern and southern) separated by an accommodation zone (Radic *et al*., 20002; Melnick *et al*. 2006). The first fossil mammals reported from the CMF were recovered from the

southern basin, near Lonquimay (Marshall *et al*., 1990; Suarez *et al*., 1990, Croft *et al*., 2003b). These sparse collections include native ungulates (*Astrapotherium*, *Nesodon*, *Protypotherium*) that collectively suggest a late early Miocene age (Santacrucian SALAMA). These initial discoveries motivated later explorations. In 2001, a team of paleontologists and geologists from the United States and Chile, including Reynaldo Charrier, Gabriel Carrasco, John Flynn, and Andre Wyss, had their prospecting efforts in the Lonquimay basin thwarted by rain and nearly impenetrable bamboo. Deterred, but not defeated, the team ventured to the northern basin, where their perseverance was rewarded after reaching LdL. During this first foray into the region, fossils were recovered from along the flanks of a ridge immediately southeast of the lake (Cerro Los Pinos). In subsequent field seasons (2002-2005), four additional collecting regions further south and east yielded abundant mammal fossils, including many well-preserved dentitions. The five principal collecting regions southeast of LdL are informally designated Cerro Los Pinos, Estero Correntoso, Estero Campamento, Estero Trapa Trapa West, and Estero Trapa Trapa East (listed from north to south) (figs. 1.4, 1.6).

The ~100 $km^2$ area southeast of LdL has been well studied geologically (Herriott, 2006; Flynn *et al*., 2008), providing a robust stratigraphic and geochronologic framework for fossils recovered from the CMF and TTF. Detailed mapping (1:20,000 scale) (fig. 1.5), combined with high precision $^{40}Ar/^{39}Ar$ ages, have enabled precise characterization and correlation of these folded volcano-sedimentary units, which are exposed at different locations throughout the region (Herrit, 2006) (figs. 1.5, 1.6). Together, these stratigraphically overlapping deposits record a ~1.9 km thick sequence of the CMF and an 800 m thick sequence of the overlying TTF (Herriott, 2006) (figs. 1.5, 1.6). Tuffs and ignimbrites fortuitously distributed throughout the CMF have yielded 14 $^{40}Ar/^{39}Ar$ dates

ranging in age from ~20 to ~14.5 Ma; in the overlying TTF, two basaltic andesite lava flows are dated to ~9 Ma (reported in Herriott, 2006; Flynn *et al*., 2008; to be more fully documented by Gans *et al*., in progress) (fig. 1.6).

The CMF, from which all but three fossils have been recovered, is composed primarily of volcaniclastic sedimentary sequences, interpreted as floodplain deposits of debris and hyperconcentrated flows associated with lahars (though channel facies fluvial deposits are also present) (Herriott, 2006). The tremendous thickness of these sequences suggests that they accumulated within an intra-arc extensional basin (Jordan *et al*., 2001; Herriott, 2006; Flynn *et al*., 2008). Kilometer-scale folds southeast of LdL make it abundantly clear that this extensional regime was later inverted (see fig. 1.4b-d) (Herriott, 2006). The pattern of deformation of the CMF suggests that extension in this region persisted until at least ~14 Ma, and that subsequent (late Miocene?) east-west shortening led to large-scale fault-propagation folding (Herriott, 2006; Flynn *et al*., 2008).

Nearly 250 fossils, including most of the dentitions treated in this study, were recovered from the CMF southeast of LdL, and an additional 15 were collected north of the lake. Most southern localities are stratigraphically well-constrained, with fossils occurring throughout most of the CMF and into the TTF (fig. 1.6). Geochronologic and biostratigraphic evidence suggests that this sequence spans as many as six SALMAs (~20-9 Ma; Colhuehuapian-?Chasicoan SALMAs) (Wertheim, 2007; Flynn *et al*., 2008). In all of South America, only the Gran Barranca section in Argentine Patagonia spans a longer time interval (~40-19 Ma; Ré *et al*., 2010; Dunn *et al*., 2013). A majority of LdL fossils were recovered from the lower units of the CMF (units $Tcm_1$ and $Tcm_2$ of Herriott, 2006) (fig. 1.6), potentially corresponding with Colhuehuapian, "Pinturan," and Santacrucian SALMAs.

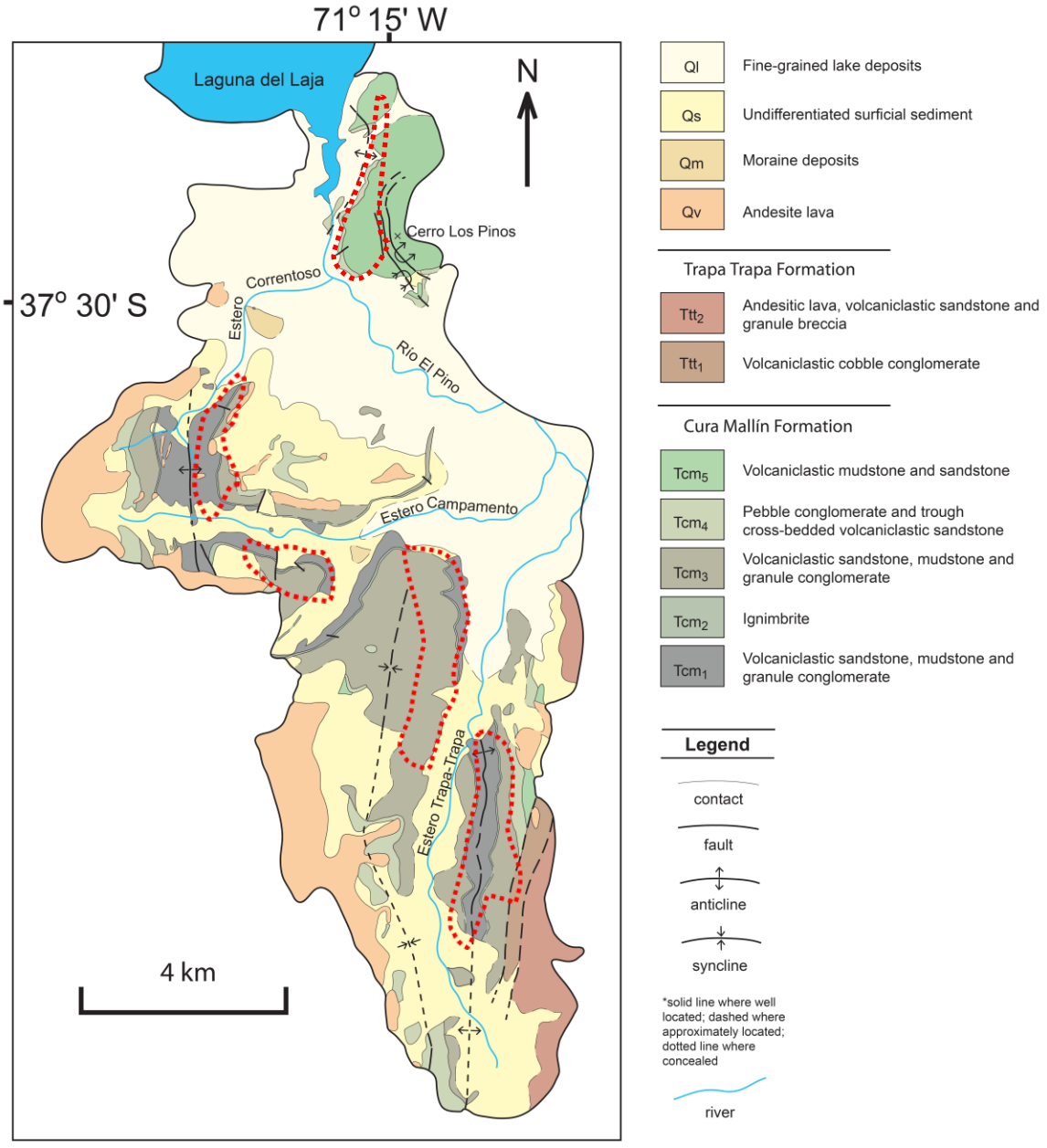
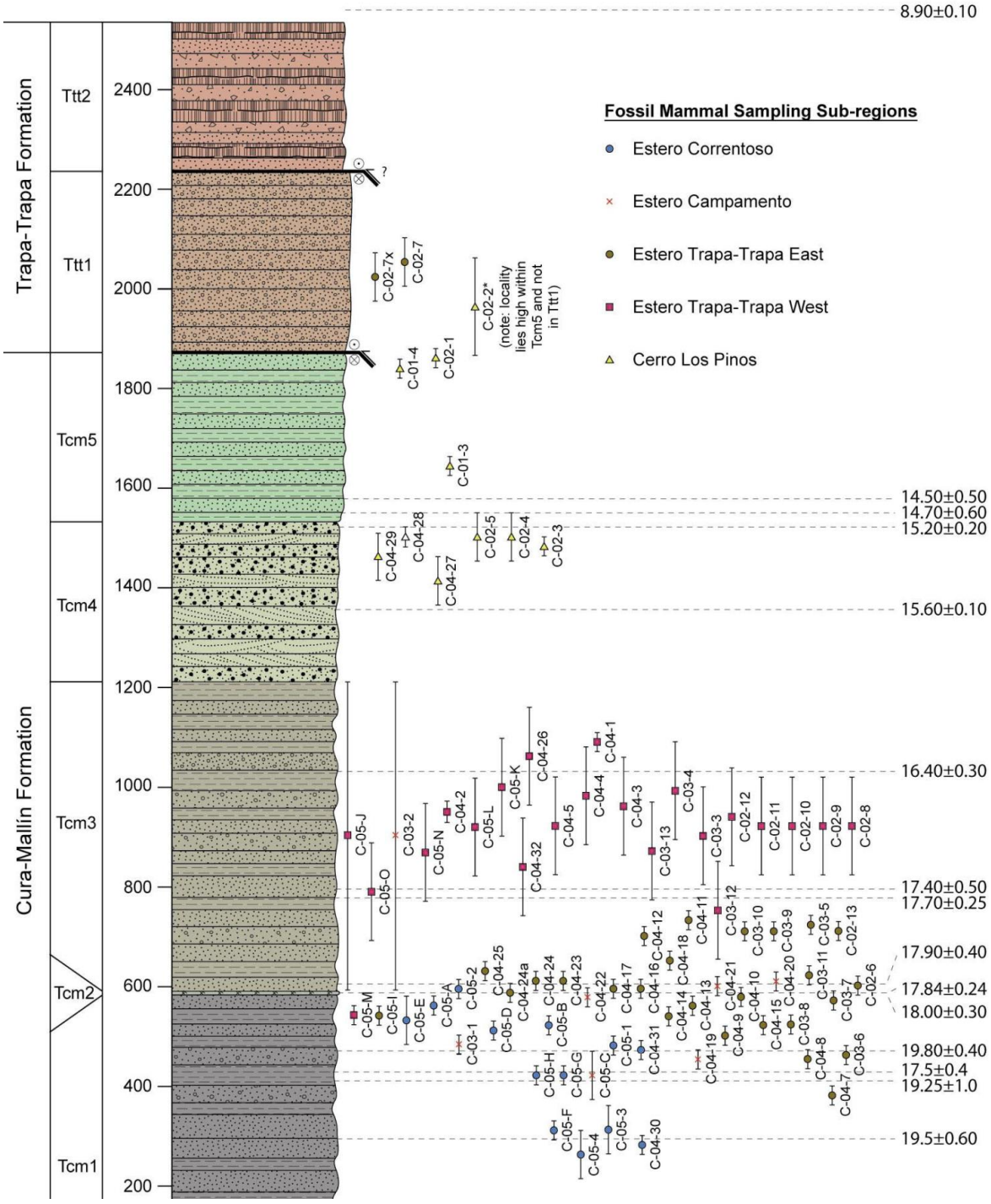



FIGURE 1.5. Map of the Laguna del Laja study area. Generalized geological map showing the volcano-sedmimentary formations (and their subunits) discussed in the text. Fossil mammal sampling subregions are encolosed by red stippled lines. These collecting regions are infromally designated (from north to south) Cerro Los Pinos, Estero Correntoso, Estero Campamento, Estero Trapa Trapa West, and Estero Trapa Trapa East. Modified from Herriot (2006) and Flynn *et al*. (2008).


Trapa-Trapa Formation
Cura-Mallín Formation
Ttt2
Ttt1
Tcm5
Tcm4
Tcm3
Tcm2
Tcm1
2400
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
Fossil Mammal Sampling Sub-regions
Estero Correntoso
Estero Campamento
Estero Trapa-Trapa East
Estero Trapa-Trapa West
Cerro Los Pinos
C-02-2* (note: locality lies high within Tcm5 and not in Ttt1)
8.90±0.10
14.50±0.50
14.70±0.60
15.20±0.20
15.60±0.10
16.40±0.30
17.40±0.50
17.70±0.25
17.90±0.40
17.84±0.24
18.00±0.30
19.80±0.40
17.5±0.4
19.25±1.0
19.5±0.60

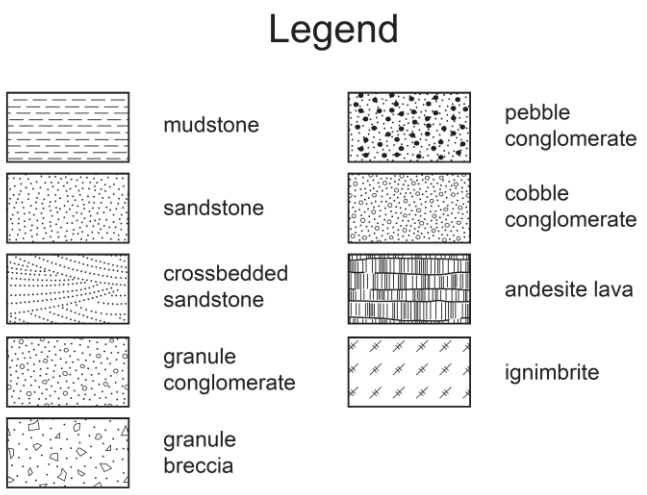



FIGURE 1.6 (including previous page). Stratigraphic column of the Cura Mallín and Trapa Trapa formations in the region southeast of Laguna del Laja (from Herriot, 2006). This is a composite of correlated strata from different locations, since the sequence is nowhere exposed in its entirety at one site. Stratigraphic positions of fossil localities are shown. Multiple fossils have been recovered from some localities, but in many cases each locality is associated with a single specimen. The vertical height of "error bars" for each locality represent the level of uncertainty in stratigraphic position (short bars = well-constrained; longer bars = moderately to poorly constrained). The stratigraphic positions of $^{40}Ar/^{39}Ar$ ages are also indicated

A preliminary report of these superposed LdL faunas is available (Flynn *et al*., 2008), but only the rodents (Wertheim, 2007) and a single native ungulate taxon (Shockey *et al*., 2012) have been described in detail previously. The latter, *Colpodon antucoensis*, represents a new species of toxodontian notoungulate and is the first record of *Colpodon* in Chile, extending the northern range of this genus (Shockey *et al*. 2012). Rodents from the LdL region exhibit a striking degree of diversity and endemism; of the 22 taxa recognized, 20 represent new species (10 of them in new genera) (Wertheim, 2007). This taxonomic novelty is especially apparent at higher stratigraphic levels, where morphological differences between LdL rodents and their coeval Patagonian counterparts become more conspicuous (Wertheim, 2007). This pattern of "increasing endemism" at LdL may correspond to the establishment of more pronounced topographic barriers, interpreted to suggest that local uplift of the Andes commenced at ~18 Ma (Wertheim, 2007). The fossil record of rodents may also document a paleoclimatic transition. The crown height of rodent dentitions from LdL increases up section, coinciding with middle Miocene global cooling (Zachos *et al*., 2001; Wertheim, 2007). Hypsodont and hypselodont dentitions are commonly interpreted to represent adaptations for grazing abrasive grasses, thus documenting the spread of arid

grasslands (Pascual and Odremán-Rivas, 1971; Pascual and Jaureguizar, 1990b; Verzi *et al.*, 1994; Pascual *et al.*, 1996; Croft, 2000, 2001; Flynn *et al.*, 2003; for additional interpretations see Stromberg *et al*., 2013; Madden, 2014). Accordingly, the development of higher crowned dentitions among LdL rodents suggests an environmental shift to drier, more open habitats (Wertheim, 2007).

Typotherian notoungulates are common at LdL, but only preliminary reports of these specimens are presently available (Flynn *et al*., 2008; Luna *et al*., 2012, 2013). Chapters 2 and 3 of this dissertation provide the first detailed descriptions and phylogenetic analyses of typotherian notoungulates from the LdL region.

Taxa of small to medium body size, including typotherians and rodents, unexpectedly constitute a significant proportion of the fossils recovered from the LdL region. A possible taphonomic explanation for this size distribution is proposed in Chapter 4.
Chapter 5 provides an updated taxonomic summary of LdL faunas, including a brief report of an additional native ungulate taxon, and discusses the biogeographical, biostratigraphic, and paleoecological implications of fossils from the LdL region.

## South American native ungulates

The "archaic" therian mammals of South America's "First Faunal Stratum" (Paleocene-Eocene) included xenarthrans, maursupials, and several groups of ungulates. These extinct ungulates – "condylarths," litopterns, xenungulates, pyrotheres, astrapotheres, and notoungulates – exhibit spectacular diversity, disparity, and dominance in the fossil record. The higher-order relationships of these groups to each other and to non-South

American ungulates remain an open question, as each new study offers a seemingly divergent interpretation (e.g. Cifelli, 1983, 1993; McKenna and Bell, 1997; Muizon and Cifelli, 2000; Horovitz, 2004; Billet, 2010, 2011; Agnolin and Chimento, 2011; Billet and Martin, 2011; O'Leary *et al*., 2013; Kramarz and Bond, 2014; Billet *et al*., 2015). "Condylarths" are almost certainly paraphyletic, likely representing a diverse assemblage of basal ungulates with affinities to several other groups (Muizon and Cifelli, 2000; Horovitz, 2004; O'Leary *et al*., 2013; Billet *et al*., 2015), including xenungulates (Gelfo *et al*., 2008). Though there is robust support for astrapothere monophyly (Kramarz and Bond, 2009; Bond *et al*., 2011; Vallejo-Pareja *et al*., 2015) the affinities of this group to other South American mammals are unclear (see multiple interpretations in Billet *et al*., 2015). Recent studies suggest that litopterns may be paraphyletic (Billet, 2010; Billet *et al*., 2015), and that pyrotheres, while monophyletic, evolved from within Notoungulata (Billet, 2010; 2011; Billet *et al*., 2015). "Condylarths," litopterns, xenungulates, astrapotheres, and notoungulates are all recorded in the Paleocene (Paula Cuoto, 1952; Soria and Powell, 1981; Muizon and Cifelli, 2000), but only astrapotheres, litopterns, and notoungulates persisted into the Miocene. Astrapotheres are last recorded in the middle Miocene (Laventan SALMA) (Johnson and Madden, 1997; Vallejo-Pareja *et al*., 2015), while notoungulates and litopterns survived into the Quaternary (Baffa, 2000 [and references therein]; MacFadden, 2005; Scherer *et al*., 2009).

Notoungulates, the primary focus of this study, are among the most diverse and abundant mammals in the South American fossil record, with ~150 genera traditionally divided into some 13 families (Cifelli, 1993; McKenna and Bell, 1997) (fig. 1.7). The study of notungulates began in 1833 with a payment of 18 pence. The buyer was Charles Darwin, the seller was a Uruguayan farmer, and the eventual recipient of the purchased skull was

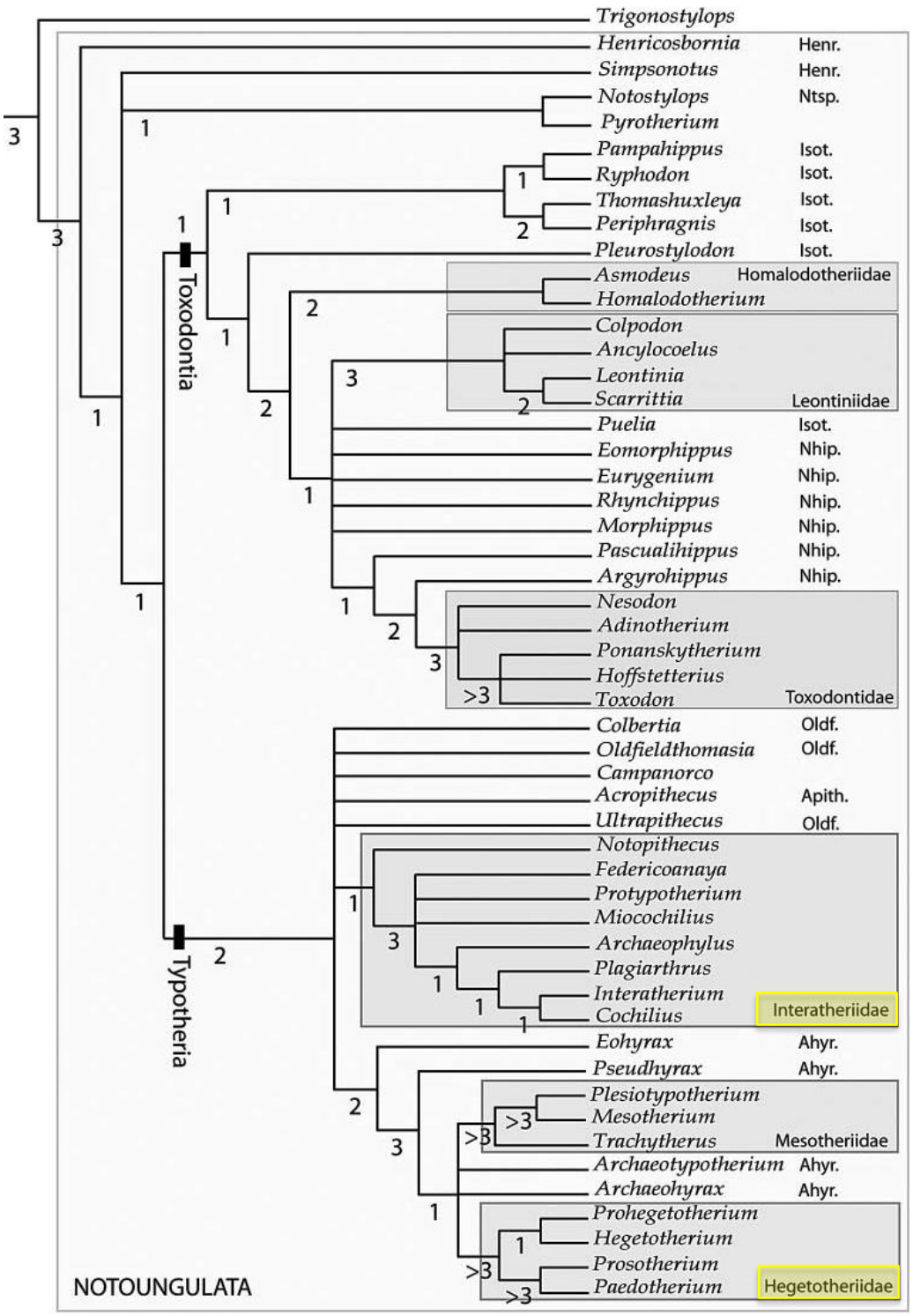



FIGURE 1.7. Phylogeny of Notoungulata (from Billet, 2009). Traditionally recognized notoungulate families are listed on the right; families corresponding to true clades are in grey boxes. Bremer Supports provided at the base of each node (1 = low support; 5 = high support). Interatheriidae and Hegetotheriidae fossils are described in Chapters 2 and 3, respectively. Abbreviations: Henr. = Henricosborniidae; Ntsp. = Notostylopidae; Nhip.= Notohippidae; Isot. = Isotemnidae; Oldf. = Oldfieldthomasiidae; Apith. = Archaeopithecidae; Ahyr. = Archaeohyracidae.

Richard Owen (Darwin, 1839). The title of Owen's (1837) study is an apt homage to the enduringly enigmatic notoungulates: "A description of the cranium of the *Toxodon platensis*, a gigantic extinct mammiferous animal, referrible [*sic*] to the Order Pachydermata, but with affinities to the Rodentia, Edentata, and Herbivorous Cetacea." Owen was the first great paleontologist to be baffled by these beasts, but he certainly would not be the last. Florentino Ameghino described the first abundant collections of notoungulate fossils, but classified these among various groups of mammals, both extant and extinct, including chalicotheres, hyraxes, equids, and primates (Ameghino, 1895, 1897, 1902, 1906). Santiago Roth, Ameghino's contemporary, recognized peculiar cranial similarities among these disparate remains, and suggested that these mammals belonged to an entirely extinct order known only to South America (Roth, 1903). This taxon is still known by the name Roth gave it: Notoungulata, the "southern ungulates."

Scores of new fossils and copious studies have significantly augmented our knowledge of notoungulates; though these efforts are too numerous to summarize here, the insightful and prolific contributions of George Gaylord Simpson (e.g., 1932, 1934, 1936, 1945, 1948, 1967) merit recognition for advancing a clear classification that continues to inform modern systematics. The first comprehensive phylogenetic analysis of South American ungulates provided robust support for notoungulate monophyly, and recognized two main sub-clades: the medium to large-sized toxodontians and the small to medium-sized typotherians (Cifelli, 1993). More recent analyses still recognize the monophyly of these clades, but include the Paleogene pyrotheres at a basal position within notounguates, based primarily on similarities of the auditory region of the skull (Billet, 2010, 2011; 2015) (fig. 1.7). These studies, along with many others (e.g., Shockey, 1997; Cerdeño and Bond, 1998; Hitz *et al*., 2000, 2006, 2008; Reguero *et al*., 2003b; Croft *et al*., 2004; Croft and Anaya,

2006; Shockey and Anaya, 2008; Billet *et al*., 2009; Reguero and Prevosti, 2010; Shockey *et al*., 2012; Kramarz and Paz, 2013), have also helped to elucidate the inter and intra-familial relationships of notoungulates (fig. 1.7).

This dissertation provides a report and description of ungulate fossils from the LdL region. Litoptern fossils have yet to be identified in these faunas, but two LdL specimens are referred to *Astrapothericulus iheringi* (an early Miocene astropothere) (CH. 5), and notoungulate skulls and dentitions, especially of typotherians, are among the most commonly recovered fossils in the region. Although toxodontian fossils are few in number, one well-preserved dentition has already been recognized as a new species, *Colpodon antucoensis* (Shockey *et al*., 2012). The present study describes the typotherian fossils recovered southeast and north of LdL (Chs. 2-3).

Three typotherian clades are known from Miocene and later faunas: hegetotheriids, mesotheriids, and interatheriids (Reguero and Prevosti, 2010; Billet, 2011). Mesotheriids have yet to be identified at LdL. In Chapter 2, I describe three new interathere species from the LdL region, one of which is conspecific with a dentition collected from Las Leñas (~240 km north northeast of LdL). Four interatheriid specimens, referred to *Protypotherium praerutilum*, prompt a preliminary revision of this genus and species (Ch. 2). Two new hegetothere species are described in Chapter 3. In addition to highlighting the geographic and taxonomic diversity of typotherians, this study helps elucidate the intra-familial relationships of hegetotheriids and interatheriids, offering new hypotheses of morphological evolution within these clades, and documenting an independent yet apparently simultaneous radiation of hypselodont interatheriids and hegetotheriids (Chs. 2-3, 5).

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Chapter 2. Early Miocene interatheriines (Interatheriidae, Typotheria, Notounuglata) from the Laguna del Laja region, with a preliminary revision of *Protypotherium* and a phylogeny of Interatheriinae

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## INTRODUCTION

Recently recovered, Miocene-aged fossils from the central Andean Main Range near Laguna del Laja (LdL), Chile, (~37.5°S, 71°W) provide a unique geographic, depositional, and chronologic framework to study the evolution of mammals in South America. Several hundred fossil mammal specimens were collected during field seasons between 2001-2005, only one of which has been formally documented (Shockey *et al*., 2012). Herein are described the interatheriines (Interatheriidae, Notoungulata) from the LdL region, providing new insights into the diversity, phylogeny, and biogeography of this clade.

The vast majority of fossils in the LdL region have been collected from a 100 $km^2$ area southeast of the lake, where steep exposures of the Cura-Mallín Formation (CMF) and overlying Trapa Trapa Formation (TTF) border several streams of the lake's southern drainage (fig. 2.1). Between ~37°S and ~39°S, the CMF and overlying units were deposited in two half-grabens separated by an accommodation zone (Radic *et al*., 2002). Sparse collections of fossil mammals had previously been reported from the CMF in the southern basin (south of ~38°S), near Lonquimay (Marshall *et al*., 1990; Suarez *et al*., 1990, Croft *et al*., 2003); the specimens described herein are among the first reported in detail from the northern sub-basin, near LdL (see also Wertheim, 2007; Shockey *et al*., 2012). Five field seasons in the LdL region have produced an abundance of well-preserved fossils from five geographically distinct, but stratigraphically overlapping collecting areas (Flynn *et al*.,

2008). These collecting areas – informally designated as Cerro Los Pinos, Estero Correntoso, Estero Campamento, Estero Trapa Trapa West, and Estero Trapa Trapa East – together preserve an 1800 m-thick sequence of the CMF (Herriott, 2006) (figs. 2.1, 2.2). This formation consists primarily of strongly folded, volcaniclastic strata, which are interpreted to have been deposited as lahars in an intra-montane basin (Herriott, 2006). Recent geologic mapping southeast of LdL has provided a detailed stratigraphic and structural framework for fossiliferous horizons within the CMF, allowing correlation between the laterally discontinuous strata exposed across the broad area of study (Herriott, 2006). In addition, interbedded ash-fall tuffs and ignimbrites occur throughout the CMF; from these units 14 high-precision, stratigraphically consistent, $^{40}Ar/^{39}Ar$ ages have been generated, showing that fossiliferous horizons of the CMF range between ~19.5-14.5 Ma in age (Herriott, 2006; Flynn *et al*., 2008). Most fossils from the LdL region have been recovered from the CMF, but there are also three specimens (one described herein) from the overlying TTF. Fossils from the TTF are not well-constrained geochronologically, but they underlie a basalt dated to ~9 Ma. The temporal span of this sequence, and the number of stratigraphically superposed mammal faunas it contains, is rivaled in all of South America only by the Gran Barranca section in Argentine Patagonia (~40-19 Ma; Ré *et al*., 2010; Dunn *et al*., 2013). The temporally calibrated stratigraphy southeast of LdL provides a robust chronologic framework for mammalian fossils collected in the region. Herein we describe the craniodental remains of interatheres (Interatheriidae, Notoungulata) that have been recovered near LdL, including three new genera, and several specimens referred to *Protypotherium praerutilum*.

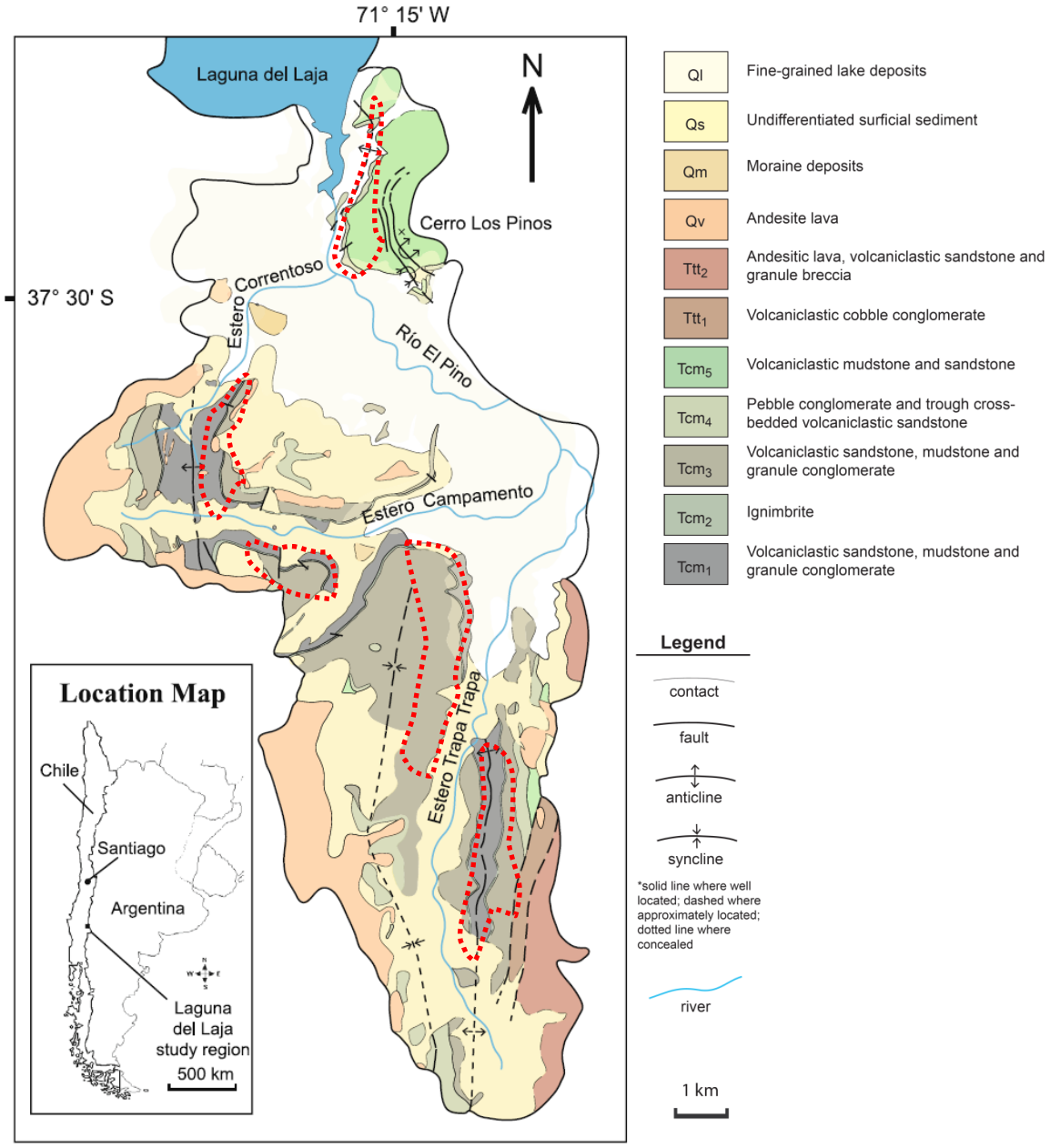


FIGURE 2.1. Map of the Laguna del Laja study area. Generalized geological map showing the sedmimentary units discussed in the text. Fossil mammal sampling subregions are encolosed by red, stippled lines. These collecting regions are infromally designated as (from north to south) Cerro Los Pinos, Estero Correntoso, Estero Campamento, Estero Trapa Trapa West, and Estero Trapa Trapa East. Inset shows the location of the study area within Chile. Modified from Herriott, 2006 and Flynn *et al*., 2008.

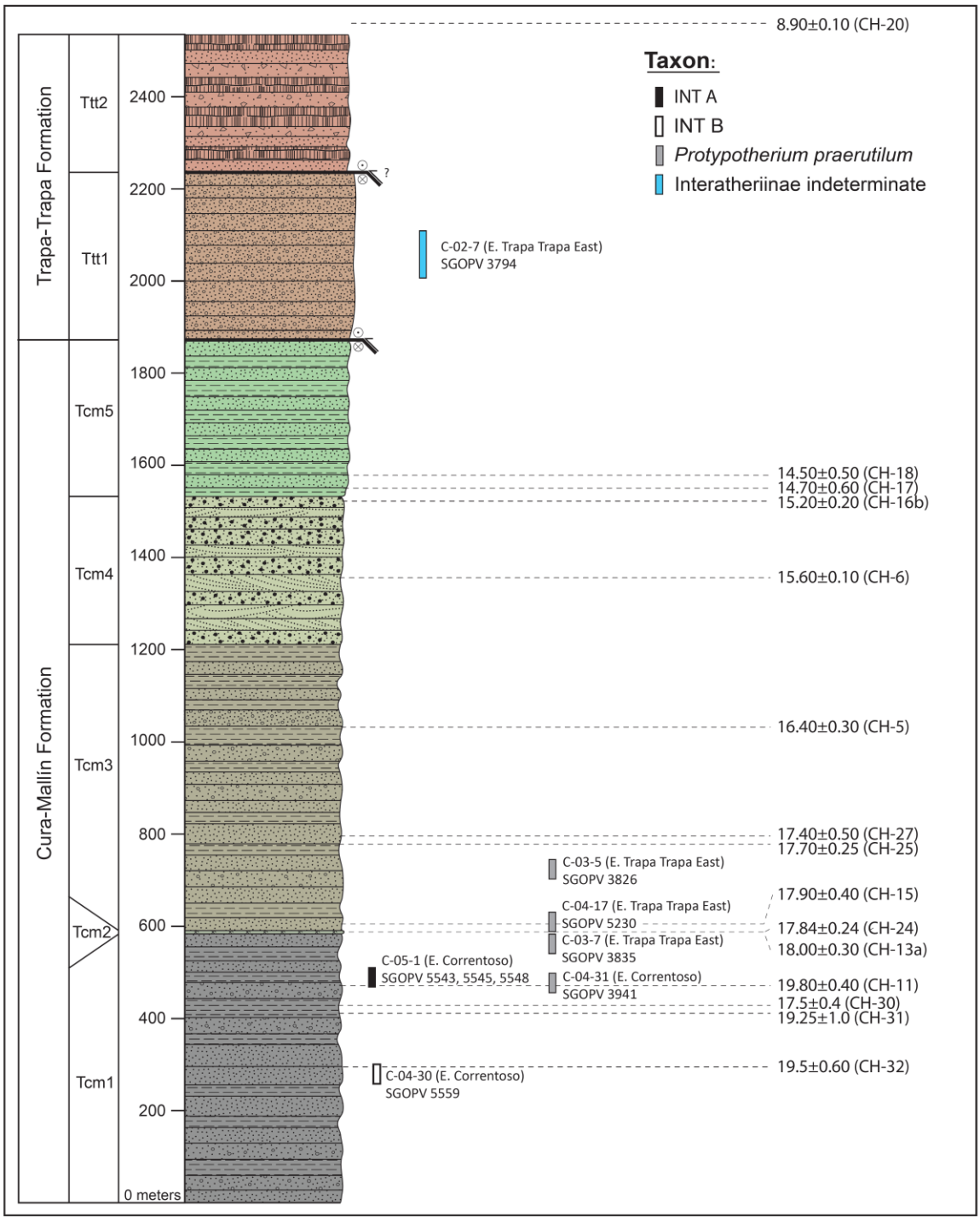


FIGURE 2.2. Composite stratigraphic section of the Cura-Mallín and Trapa Trapa formations exposed in the region southeast of Laguna del Laja. On the right, $^{40}Ar/^{39}Ar$ dates are indicated, with samples used for radioisotope analyses in parantheses. Stratigraphic positions of interatheriid specimens inlcude locality numbers (with collecting regions in parantheses) and specimen numbers (SGOPV). The vertical height of bars associated with each specimen/locality represent the level uncertainty in stratigraphic position, with short bars indicating well-constrained stratigraphic positions and longer bars indicating moderately constrained stratigraphic positions. See fig. 1.6 for stratigraphic column legened.

Three specimens discussed in this study were collected from slightly different stratigraphic and/or geographic settings: A partial mandibular symphysis (SGOPV 3794) tentatively referred to Interatheriinae, was recovered from the Trapa Trapa Formation (TTF) at EsteroTrapa Trapa East (locality C-02-7). The TTF conformably overlies the CMF, and consists primarily of andesites, basalts, and volcaniclastic conglomerates and breccias (Herriot, 2006). This fragmentary dentition is one of only three specimens recovered from the TTF. While the vast majority of specimens from the LdL region have been collected southeast of the lake, one dentition described herein (SGOPV 3974) originated in an outcrop of the CMF ~6 km north of the lake (locality C-04-36). The precise stratigraphic position of this locality relative to the temporally constrained stratigraphy southeast of the lake remains uncertain. Although the age of SGOPV 3974 is unknown directly, a conspecific specimen from a locality ~300 km NNE of LdL, described herein, is precisely dated. This latter specimen (SGOPV 3210), also from the Andes of central Chile, was recovered from steep exposures of the Abanico Formation along the southern flank of Río Las Leñas (from the same large, volcaniclastic talus block, in fact, that yielded the holotype of *Chilecebus carrascoensis*; Flynn *et al*., 1995). An $^{40}Ar/^{39}Ar$ analysis from this block indicates an age of ~20.09 Ma (Flynn *et al*., 1995).

Interathere fossils are among the most commonly recovered specimens from the LdL region. Interatheres are a diverse clade of small to medium-sized notoungulates that are generally well represented throughout most of the Cenozoic of South America. The earliest known interatheres are small, brachyodont taxa from the ?Itaborian South American Land Mammal "Age" (SALMA) (?mid Paleocene) (Bond *et al*., 1995). These brachyodont forms – which have traditionally been grouped in the "Notopithecinae" (Simpson, 1945; McKenna and Bell, 1997) – persist into the Tinguiririan (early Oligocene) (Wyss *et al*., 1994; Hitz *et*

*al*., 2006). Hypsodont interatheres first appear in the early Oligocene Tinguiririan SALMA (Wyss *et al*. 1994; Hitz *et al*., 2000) and are last recorded in the Late Miocene (the "Conglomerado osífero" of the Ituzaingó Formation [Ameghino 1885], which may correspond temporally to the Huayquerian SALMA [Cione *et al*., 2000]). Hypsodont and hypselodont interatheres have traditionally been allocated to the Interatheriinae (Simpson, 1945), and indeed several recent phylogenetic analyses suggest that hypsodonty is diagnostic of the clade (Reguero *et al*., 2003; Reguero and Prevosti, 2010; this study). While cladistic analyses suggest that notopithecines are paraphyletic (Hitz *et al*., 2000, 2006; Reguero *et al*., 2003; Reguero and Prevosti, 2010), there is strong support for interatheriine monophyly (Cifelli, 1993; Hitz *et al*., 2000, 2006, 2008; Reguero and Prevosti, 2010).

Miocene interatheriines – most notably *Protypotherium*, *Cochilius*, and *Interatherium* – have long been well known from Argentine Patagonia (e.g., Ameghino, 1885, 1887a, 1887b, 1889, 1891, 1894, 1902; Sinclair 1909; Simpson, 1932a, 1932b). Despite well-preserved and abundant collections of these taxa housed at several museums, or perhaps partly because of the wide dispersion of this wealth of material, the taxonomy of these genera and their constituent species is long overdue for critical reevaluation. Since three specimens recovered from near LdL are clearly assignable to *Protypotherium*, we undertook an extensive examination of *Protypotherium* fossils housed at museums in Buenos Aires, La Plata, Córdoba, New York, and New Haven (as well as smaller collections elsewhere), which allowed us to clarify several lingering taxonomic problems and ambiguities. Accordingly, we offer a preliminary revision of *Protypotherium* in the hope that it spurs further critical reappraisal of this well-known genus.

In addition to significant intereatheriine collections from Argentine Patagonia, a steadily growing number of extra-Patagonian fossil localities in Colombia (Striton, 1953),

Chile (Hitz *et al*., 2000, 2006), and Bolivia (Croft, 2007; Hitz *et al*., 2008) have begun to reveal a fuller sense of the taxonomic and geographic diversity of this clade, and recent phylogenetic analyses (Cifelli, 1993; Hitz *et al*., 2000, 2006, 2008; Reguero *et al*., 2003; Reguero and Prevosti, 2010) have provided a more robust understanding of interatheriine relationships. Still, these recent phylogentic results are plagued by a lack of resolution (Cifelli, 1993; Hitz *et al*., 2000, 2006, 2008), contradictory results (e.g., compare Hitz *et al*., 2000, 2006, 2008, and Reguero *et al*., 2003), and/or the exclusion of key taxa (e.g., Reguero and Prevosti, 2010). The taxonomic and phylogenetic work presented herein contributes to this growing body of knowledge.

## MATERIALS, ABBREVIATIONS, AND METHODS

MATERIALS. The primary impetus for this study was the recent recovery (2001-2005) of several hundred fossil mammal specimens from the Laguna del Laja region. The interatheres of these LdL faunas are described, identified, and discussed herein. One specimen (SGOPV 3210), the holotype of Interatheriidae gen. *et* sp. *nov*. A, is not from LdL, but was recovered from along the Río Las Leñas drainage, ~300 km north-northeast of LdL. These specimens will be accessioned in the fossil vertebrate collection of the Museo Nacional de Historia Natural, Santiago, Chile (SGOPV). Other specimens from which data were obtained, and the publications used for scoring characters, are listed in appendices 2.2 and 2.4.

ABBREVIATIONS. The following institutions (with corresponding abbreviations used throughout this text) provided access to specimens examined in this study: American Museum of Natural History, New York (AMNH); Museo de Paleontología, Facultad de

Ciencias Exactas, Físicas y Naturals, de la Universidad de Córdoba, Córdoba, Argentina (CORD-PZ); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina (MACN; MACN-A refers to specimens that belong to the Ameghino collection); Museo de La Plata, La Plata, Argentina (MLP); University of California Museum of Paleontology, Berkeley (UCMP); Yale Peabody Museum, Princeton University Collection, New Haven (YPM-PU). In addition, specimen information was obtained from contacts at the Museum of Natural History, University of Kansas, Lawrence (KUPV) and the Zoological Museum, University of Coppenhagen, Denmark (ZMUC ZMK).

The following abbreviations apply to dental descriptions: I/i for upper and lower incisors, C/c for upper and lower canines, P/p for upper and lower premolars, and M/m for upper and lower molars. Descriptions of dental morphology generally reflect the nomenclature of Reguero *et al*. (2003; see references and fig. 2 therein). Following Smith and Dodson (2003), dental orientation is indicated by four cardinal directions: mesial, distal, lingual, and labial. All measurements were obtained with KÖLN calipers. Mesiodistal dimensions (lengths) of teeth were obtained at the greatest length of the ectoloph (these are equivalent to measurements 8 [lower teeth] and 11 [upper teeth] in fig. 5 of Tauber [1996]). Labiolingual dimensions (transverse widths) of cheek teeth were obtained by measuring the maximum width between the ectoloph and entoloph, perpendicular to the mesiodistal orientation of the tooth (for cheek teeth, this is equivalent to measurements 3 [lower teeth] and 12 [upper teeth] in fig. 5 of Tauber [1996]). A recent illustration of these tooth measurements is also provided by Billet *et al*. (2009; fig. 1 therein). Palatal length was measured along the midline (sagittal axis) of the palate, from the posterior margin of I1 (or I1 alveolus) to the posterior margin of M3 (at the point at which a transverse line at the

posterior margin of M3 intersects the midline of the palate). Palatal width was measured between the lingual margins of the left and right M1 paralophs.

METHODS. Our cladistic analysis of interatheriines incorporates 18 taxa, including the three described in the present study, and all those regarded as interatheriines by Reguero *et al*. (2003, 2010) and Hitz *et al*. (2000, 2006, 2008). This includes *Eopachyrucos* and *Proargyrohyrax* (not considered interateheriines by Hitz *et al*., 2006, 2008), consistent with our preferred definition of Interatheriinae (*sensu* Reguero *et al*., 2003) as the clade stemming from the last common ancestor of *Eopachyrucos* and *Interatherium*. In addition, we include *Johnbell hatcheri* and *Ignigena minisculus* in our analysis, as these taxa were supported as proximal outgroups to the Interatheriinae (*sensu* Reguero *et al*., 2003) by Hitz *et al*. (2000, 2006). Finally, *Notopithecus*, which has consistently been identified as the earliest diverging interathere (Hitz *et al*., 2000, 2006; Reguero *et al*., 2003; Reguero and Prevosti, 2010) is included as an outgroup to all other taxa. Taxa were coded for 40 characters – 32 dental and 8 cranial (appendices 2.1, 2.2). Many of the characters examined were obtained from published studies (Hitz *et al*., 2006; Reguero *et al*., 2003), but several character descriptions and codings were revised to increase clarity or to incorporate new observations. Appendix 2.1 includes a detailed character list discussing differences from previous studies.

A parsimony analysis was performed with "Tree analysis using New Technology" (TNT) v1.1 (Goloboff *et al*., 2003, 2008). Given the high degree of homoplasy observed in previous studies (Cifelli, 1993; Hitz *et al*. 2000, 2006; Reguero *et al*., 2003), character weights were determined using implied weighting (k=3), which estimates the reliability of characters during tree search (Goloboff, 1993); all characters were treated as unordered. A "New technology search" using Sectorial Search and Tree Fusing (Goloboff, 1999, Goloboff *et al*., 2008) yielded three equally parsimonious trees. Support for each node of the consensus tree

was determined with Symmetric Resampling (P=33) (Goloboff *et al*., 2003), using 500 replicates with Tree Bisection Reconnection (TBR) as the swapping algorithm (Goloboff and Farris, 2001).

Isotopic ages of tuffs, ignimbrites, and lava flows from the LdL region are reported by Herriot (2006) and Flynn *et al*. (2008), and the methods and results of these analyses will be more fully documented by Gans *et al*. (in progress).

## SYSTEMATIC PALEONTOLOGY

NOTOUNGULATA Roth, 1903

TYPOTHERIA Zittel, 1893

INTERATHERIIDAE Ameghino, 1887a

INTERATHERIINAE Ameghino, 1887a

Interatheriinae gen. *et* sp. *nov*. A

Fig. 2.3, table 2.1

SYNONYMY: "Interatheriinae, unident.," Flynn *et al*. 2008: table 1

HOLOTYPE: SGOPV 5545 consists of a nearly complete pair of mandibles, only the left one of which has been prepared, exposing i1-m3. With the exception of the i1, the right dentition remains encased in matrix.

REFERRED MATERIAL: One additional specimen recovered from the same locality as the holotype is referred to this taxon: SGOPV 5548, a partial skull with a nearly complete right mandible in occlusion with the right P2-M3 (only the ectolophs of P2-M3 are visible,

and these upper cheek teeth obscure most of the lower right dentition, except for the well preserved i1-C), and partial left mandible bearing i1, partial p2, p3-m2, and partial m3.

QUESTIONABLY REFERRED MATERIAL: SGOPV 5543, a partial left mandible bearing p4-m3.

DISTRIBUTION AND AGE: Known only from the type locality, Estero Correntoso site C-05-1, south of Laguna del Laja (LdL), in the Andes of central Chile (figs. 2.1, 2.2). The holotype (SGOPV 5545) and referred specimens (SGOPV 5548, 5543) were recovered from the lowest exposed member of the Cura-Mallín Formation (unit $Tcm_1$, Herriott, 2006) in the LdL region. Site C-05-1 is bracketed by two ashes—a 1 m thick ash-fall tuff just a few meters below the fossils, and a 10 m thick ignimbrite ($Tcm_2$) about 100 m above (fig. 2.2). The underlying ash fall tuff (CH-11) yielded a preferred age of 19.80 ± 0.40 Ma, while two samples of the overlying ignimbrite yielded preferred ages of 17.84 ± 0.24 Ma (CH-24) and 18.00 ± 0.30 Ma (CH-13a) (fig. 2.2). Given the proximity of the fossil-bearing horizon to the underlying ash, the age of these fossils is likely around 19.5 Ma.

DIAGNOSIS: The primary diagnosis of Interatheriinae gen. *et* sp. *nov*. A (informally referred to herein as INT A) is based on the holotype (SGOPV 5545), and therefore includes only characters of the lower dentition (fig. 2.3). Derived characters distinguishing INT A from earlier diverging interatheriines (see figs. 2.9-11 for the phylogenetic analysis of the present study) include hypselodont molars (the molars of *Eopachyrucos, Proargyrohyrax,* and *Santiagorothia* are hypsodont but not hypselodont); procumbent lower incisors (in contrast to the more vertically implanted lower incisors of *Eopachyrucos, Proargyrohyrax*, *Santiagorothia, Brucemacfaddenia*, and *Plagiarthus*); and the absence of a persistent lingual sulcus and distinct metacristid on the lower molar trigonids (in contrast to *Eopachyrucos*, *Proargyrohyrax, Santiagorothia, Brucemacfaddenia*, and *Plagiarthus*). Beyond this, INT A

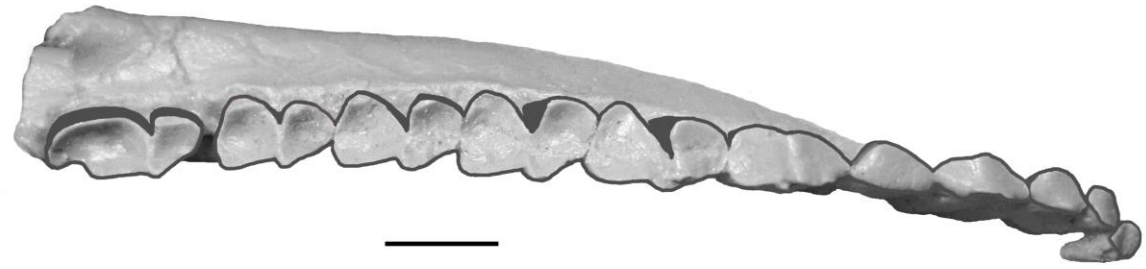

FIGURE 2.3. Holotype of Interatheriinae gen. *et* sp. *nov*. A, SGOPV 5545, a partial left mandible bearing i1-m3, shown in occlusal view. Sclae bar = 0.5 cm.

**TABLE 2.1: Dental measurements (mm) for lower dentition of INT A.**
MD = mesiodistal; LL = labiolingual

| Tooth | SGOPV 5545 | SGOPV 5548 | SGOPV 5543 |
|---|---|---|---|
| i1 MD | 1.91 | 1.86 | |
| i1 LL | 2.34 | 1.84 | |
| i2 MD | 2.27 | 1.98 | |
| i2 LL | 2.02 | 1.78 | |
| i3 MD | 3.17 | 2.74 | |
| i3 LL | 2.03 | 1.99 | |
| c MD | 4.58 | | |
| c LL | 2.14 | 2.35 | |
| p1 MD | 3.95 | | |
| p1 LL | 2.61 | | |
| p2 MD | 5.44 | | |
| p2 LL | 2.86 | | |
| p3 MD | 6.28 | 6.29 | |
| p3 LL | 3.91 | 3.64 | |
| p4 MD | 6.47 | 5.99 | 5.5* |
| p4 LL | 3.94 | 3.88 | 3.2* |
| m1 MD | 6.43 | 6.11 | 5.82 |
| m1 LL | 3.82 | 3.89 | 3.3* |
| m2 MD | 6.16 | 5.32 | 5.72 |
| m2 LL | 3.51 | 4.24 | 3.2* |
| m3 MD | 7.76 | 7.64 | 7.34 |
| m3 LL | 3.01 | | 2.9* |

*measurement approximate.

possesses a suite of characters that are often similar individually to those observed in other Deseadan and post-Deseadan interatheriines, but these characters occur in a unique combination in this taxon. In particular, INT A has numerous similarities to *Protypotherium*, including size (within the range of *P. austral* and *P. praerutilum*); m2-3 trigonids that are somewhat triangular in outline, with narrow anterior margins (also characteristic of *Protypotherium* and *Progaleopithecus*); lower molar talonids that are larger than the trigonids (as in *Protypotherium*, *Interatherium*, and *Cochilius*); and m3 talonids with a salient lingual sulcus (as in all interatheriines with known lower dentitions except for *Cochilius*, *Archaeophylus*, *Interatherium*, and *Miocochilius*). But unlike *Protypotherium* (and unlike most other interatheriines), INT A has relatively large p2-4 talonids, with the p2 talonid and trigonid subequal in size, and p3-4 talonids that are larger than the corresponding trigonids (a condition otherwise observed only in *Interatherium* and *Cochilius*). The i1-2 of INT A are columnar, appearing circular in occlusal view, as in *Protypotherium*, *Progaleopithecus*, and *Federicoanaya* (note that i1 in *Miocochilius* is similar in shape, but i2 of this taxon approaches the broader form observed in other interatheres). Although the size of the teeth increases from i1-p1, as in most interatheres, the canine and first premolar are notably smaller than p2, similar to the condition in *Plagiarthus* and *Miocochilius* (hypselodont interatheriines), as well as in *Santiagorothia* and *Eopachyrucos* (more basal interatheriines).

DESCRIPTION: The preserved dentition and skull fragments of INT A (fig. 2.3) belong to a medium-sized interatheriine, comparable in dimensions to *Brucemacfaddenia* and *Protypotherium* (intermediate between *P. praerutilum* and *P. australe*). Compared to other well-known interatheriines, INT A possesses a longer dental series than in *Federicoanaya*, *Cochilius*, and *Interatherium*, and shorter than in *Santiagorothia*, and *Miocochilius*.

The lower incisors and canine are procumbent, as in all Deseadan and post-Deseadan interatheriines except *Plagiarthus* (comparisons with *Plagiarthus* lower incisors based on Reguero, 1999 and Reguero *et al*., 2003). The i1-2 are columnar, such that they appear circular in occlusal view, and are thus similar to the incisors of *Protypotherium* (and to an extent *Federicoanaya* and *Progaleopithecus*, but the i1-2 of these taxa are better known from early wear stages that cannot be directly compared to INT A). In *Protypotherium*, *Progaleopithecus,* and *Federicoanaya*, i1-2 are initially bicolumnar, but this pair of "tines" is not persistent to the roots, such that these teeth eventually become simple columns with wear (instead of broad and lingually grooved, as in most other interatheres). Accordingly, the incisors of INT A may also have been bicolumnar early in wear. Whereas i1-2 are columnar, the i3 and canine become progressively broader – longer mesiodistally than labiolingually. The i3 is smooth and rounded on both the labial and lingual faces. The canine is smooth lingually; a very shallow vertical sulcus occurs variably on the labial surface (appearing on the type specimen, SGOPV 5545, but not on SGOPV 5548). This labial excavation of the canine likely becomes more subtle and eventually disappears with wear, given that it is less distinct rootward in SGOPV 5545. When present, this sulcus gives the canine the appearance of possessing a small talonid.

The p1 is similar in mesiodistal length to the canine, but is notably wider labiolingually. The lingual face of the p1 is smooth and flat, while the labial face is smooth and rounded. As a result, the occlusal surface of the p1 appears as an almost perfect semi-circle. The p2 is significantly longer labiolingully than p1, and bears a distinct and broad talonid. The p2 trigonid is very narrow anteriorly, and broad posteriorly, lending its occlusal surface a triangular outline. The trigonid meets the talonid at a broad transverse ridge (the metaloph) that spans almost the entire labiolingual width of the tooth; the occlusal surface of

the talonid is sloped sharply posterior to the metaloph as the result of wear. The talonid is roughly quadrangular in occlusal view, its labial margin being somewhat rounded. Along the labial surface of p2, the talonid and trigonid are separated by a deep vertical sulcus that descends from the metaloph. In labial view, the trignoid is notably longer than the talonid, but in occlusal view the trigonid and talonid have similar surface areas, primarily reflecting their differences in shape (the former being triangular and the latter somewhat quadrangular). In possessing a short but distinct and broad p2 talonid, INT A most resembles *Cochilius*. The lingual surface of p2 also bears a vertical sulcus separating the trigonid and talonid, but it is shallower than the corresponding labial sulcus. Anterior to this lingual sulcus occur two even subtler vertical grooves; in combination, the sulcus and grooves give the lingual surface of the p2 a striated appearance. The p3 and p4 are very similar, differing primarily in the shape of the trigonid. The p3 trigonid is nearly triangular in occlusal view, broad posteriorly at the metaloph and narrowing anteriorly (similar to p2), except that the anterior margin merges into the p2 talonid before coming to a distinct "point." The p4 trigonid is nearly semicircular, with a broad, transverse metaloph and rounded anterior margin. The p4 trigonid differs from a true semicircle in being broader labially than lingually. On p3 and p4 the occlusal surface of the trigonid appears as an elevated pedestal next to the talonid, which slopes postero-labially. The p3 and p4 talonids are roughly triangular, with the anterior "apex" of this triangle attaching to the trigonid along the metaloph, just labial to the metaconid. The p3-4 talonids are large (slightly larger than the trigonids in both occlusal surface area and mesiodistal length), and are separated from the trigonids labially and lingually by deep sulci. The relatively large premolar talonids in INT A recall the morphologies observed in *Cochilius* and *Interatherium*.

The m1-2 are very similar to each other and to p4. In particular, m1 and p4 are nearly indistinguishable: their trigonids are elevated and rounded anteriorly (and hence somewhat semi-circular in occlusal view); a large, triangular talonid attaches to the metaloph just labially of the metaconid and slopes postero-labially; and deep sulci opposite each other separate the trigonid and talonid labially and lingually. The m2 is generally similar, but its trigonid is slightly more triangular, coming to a more distinct point anteriorly, where it abuts m1. Also, compared to p3-m1, the m2 trigonid is less elevated with respect to the talonid. Still, the metalophid rises steeply as it approaches the metaconid (a raised metaconid also occurs in m1, but it is more pronounced in m2). In SGOPV 5545 a small diastema separates m2 and m3, a gap that is absent in SGOPV 5548. Similar small diastemata are variably present in several species of interatheres (for example, in one *Miocochilius* specimen, AMNH 45882, a similar diastema occurs between the m2 and m3 on the left side of the specimen but not on the right). The m3 trigonid, although slightly more curved anteriorly than in m2, resembles m2 in bearing a distinct anterior apex. The subtriangular trigonids of m2-3 resemble those of *Protypotherium* and *Progaleopithecus*. The m3 metalophid rises steeply towards the metaconid (mimicking the wear pattern on m2). The m3 talonid is more than twice the mesiodistal length of the trigonid; the talonid does not slope below the level of the trigonid (as is typical of p2-m1). The talonid is roughly ovoid, and attaches to the trigonid just labially of the metaconid. The labial margin of the talonid is evenly rounded, and the labial ectoloph smooth. Most of the lingual margin of the talonid is elevated, forming a nearly continuous ridge from the metaconid to the level of the entoconid. Between the entoconid and the hypoconulid a salient sulcus, which apparently persists through wear, interrupts the generally ovoid form of the talonid. SGOPV 5548 exposes the deep portions of m3, indicating that this tooth is hypselodont. This observation, combined with premolar and

molar characteristics that are similar to those seen in other "advanced" interatheriines, suggest that the molars and posterior premolars of INT A are also hypselodont.

REMARKS: SGOPV 5548 provides further insight into the upper dentition and skull of this taxon, but as these elements are obscured or fragmentary they cannot be described in detail and reveal no morphology unique to this taxon. It is, however, notable that P2-4 bear distinct and similarly sized inflections between the paracone and parastyle – a condition observed in many interatheriines, but differing from Interatheriinae gen. *et* sp. *nov*. B (described herein; informally referred to as INT B), *Archaeophylus*, and *Brucemacfaddenia*. In addition, the upper molar ectolophs are quite smooth, as in most interatheriines, and they lack the numerous salient grooves that help diagnose INT B. These two features of the upper dentition in SGOPV 5548 allow us to confidently recognize INT A and INT B as distinct taxa, even though both are similar in size, with INT A best known from its lower dentition and INT B only represented by upper teeth. Although the degree of molarization of P2-4 in INT A cannot be definitively ascertained, the broad ectolophs of the upper premolars suggest that either some or all of these teeth may have been molariform, as in *Archaeophylus*, *Interatherium*, *Plagiarthus*, *Cochilius*, *Santiagorothia*, *Brucemacfaddenia*, *Proargyrohyrax*, INT B, and Interatheriinae gen. *et* sp. *nov*. C (described herein; informally referred to as INT C). The correlation between broad ectolophs and molariform premolars is not absolute, however, as *Miocochilius* has relatively broad ectolophs yet premolariform premolars. Perhaps the most important observation with regard to the premolars is that the large premolar ectolophs in INT A are markedly different from the relatively small ectolophs of *Protypotherium*.

Interatheriinae gen. *et* sp. *nov*. B

Fig. 2.4, table 2.2

SYNONYMY: "Interatheriinae, unident.," Flynn *et al*. 2008: table 1

HOLOTYPE: SGOPV 5559, a partial skull with nearly complete upper right dentition (well-preserved I1-C and P3-M3, but lacking P1-2; we suggest P1 is lost in this taxon, and P2 is simply missing in this specimen - see discussion in Description) and well-preserved, left I2. The left I3, C, and P2-M3 are very fragmentary. The ventral surfaces of the auditory bullae, occipital condyles, and zygomatic arches are partially exposed, but these features are poorly preserved.

REFERRED MATERIAL: This taxon is based solely on the holotype.

DISTRIBUTION AND AGE: Known only from the type locality, Estero Correntoso site C-04-30, immediately south of Laguna del Laja (LdL), in the Andes of central Chile (figs. 2.1, 2.2). The holotype was recovered from a volcaniclastic mudstone within the stratigraphically lowest exposures of the Cura-Mallín Formation in the LdL region (unit $Tcm_1$; Herriott, 2006). Site C-04-30 lies about 200 m stratigraphically below the locality from which SGOPV 5545 and 5548 (INT A) were recovered, and within a few meters of an ash fall tuff (CH-32) that yielded an $^{40}Ar/^{39}Ar$ age of 19.50 ± 0.6 Ma (Flynn *et al*., 2008) (fig. 2.2). Given the proximity of the fossil-bearing horizon to this tuff, the age of these fossils is likely very near 19.5 Ma.

DIAGNOSIS: The diagnosis of Interatheriinae gen. *et* sp. *nov*. B (informally referred to as INT B) is necessarily limited to characters of the upper dentition (fig. 2.4). Derived characters distinguishing INT B from more basal, pre-Deseadan interatheriines (e.g., *Eopachyrucos*, *Proargyrohyrax*, and *Santiagorothia*; see figs. 2.9-11 for phylogenetic results) include hypselodont molars and premolars (see discussion in Description), and cheek

teeth that maintain a persistent lingual sulcus, but lose all traces of the anteroexternal and posteroexternal sulci with wear. P3 of INT B is premolariform, as in *Miocochilius*, *Protypotherium*, and *Federicoanaya* (as well as in most pre-Deseadan interatheres). The P4, however, is large and molariform, resembling its counterparts in *Cochilius*, *Interatherium*, *Archaeophylus*, *Plagiarthus*, *Brucemacfaddenia*, *Santiagorothia*, *Proargyrohyrax*, and Interatheriidae gen. *et* sp. *nov*. C (described herein; informally referred to as INT C). This combination of a premolariform P3 and molariform P4 is unique to INT B among interatheres. INT B also uniquely possesses several shallow vertical grooves on the ectolophs of P4-M3, lending these surfaces a striated appearance, particularly on M2-3. A small diastema (~1.5 mm) occurs between I2-3, a feature shared with *Miocochilius* and variably in *Protypotherium praerutilum* and *P. australe* (thereby limiting the diagnostic utility of this feature).

INT B is further diagnosed by loss of an anterior premolar, likely P1 (the locus of this tooth is more fully discussed in the description). An apparent alveolus for P1 is not present, nor does there appear to be space in the tooth row that would have accommodated this tooth. This complete loss of P1 is unique among interatheres (note that I3 and/or C is lost in some specimens of *Interatherium*).

DESCRIPTION: The dentition and skull fragments of INT B (fig. 2.4) pertain to a medium-sized interatheriine, comparable in dimensions to *Brucemacfaddenia*, *Protypotherium* (especially *P. praerutilum*), *Cochilius*, INT A, and INT C (the latter two taxa are described herein). Compared to other well-known interatheres, the dental series of INT B is longer than in *Federicoanaya* and *Interatherium*, but shorter than in *Santiagorothia*, and *Miocochilius.*

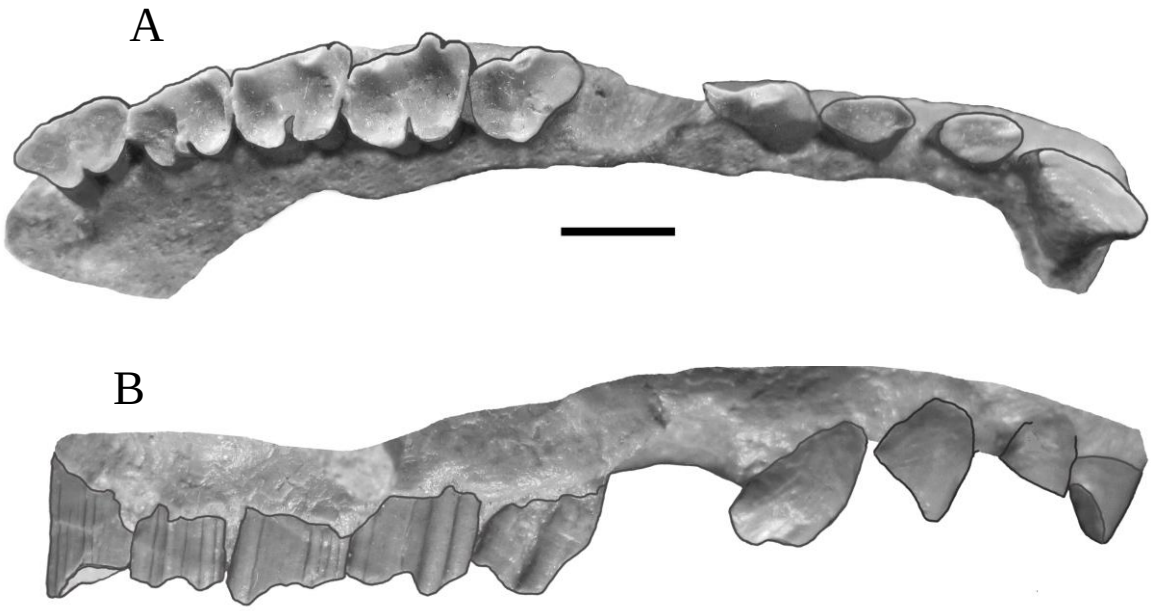


FIGURE 2.4. Holotype of of Interatheriinae gen. *et* sp. *nov*. B, SGOPV 5559, right I3-C and P3-M3. **A**: Occlusal view; **B:** Labial view. Sclae bar = 0.5 cm.

**TABLE 2.2: Dental Measurements (mm) of SGOPV 5559, holotype of INT B.**
MD = mesiodistal; LL = labiolingual

| Tooth | MD | LL |
|---|---|---|
| I1 | 5.47 | 1.66 |
| I2 | 3.99 | 2.41 |
| I3 | 3.94 | 2.28 |
| C | 3.64 | 2.26 |
| P3 | 4.69 | 3.71 |
| P4 | 5.24 | 4.37 |
| M1 | 5.09 | 3.84 |
| M2 | 4.52 | 3.44 |
| M3 | 4.62 | 3.08 |

The I1 is large, mesiodistally long but labiolingually narrow, with a smooth, convex labial surface. The distal margin of the tooth bends posteriorly at a sharp angle (as in some specimens of *Protypotherium australe* – where this feature is variably present). The I2-3 are similar in size and shape, ovoid in occlusal outline with smooth labial and lingual surfaces; both teeth are significantly shorter mesiodistally than I1. The wear surfaces of I2-3 are steeply inclined, sloping posteriorly; this is more pronounced in I3. The upper canine, similar in size to I2-3, appears to have freshly erupted, based on its limited wear. Its roughly ovoid column tapers into an anteroposteriorly directed ridge that is labially concave. The tapered ridge and labial concavity would likely be quickly lost with wear, resulting in an ovoid occlusal surface very similar to I2-3.

A large alveolus, probably for P2, occurs posterior to the canine. On the right side of SGOPV 5559 this alveolus lacks any trace of a tooth, but the left alveolus bears traces of dentine that resemble the occlusal outline of P3. This apparent similarity suggests that the alveolus would bear P2 rather than P1, since in nearly all interatheres P1 closely resembles the canine in size and shape (the notable exception being *Interatherium*, where the upper canine is highly reduced), whereas P2 more generally resembles P3. Thus, while the holotype (SGOPV 5559) preserves some evidence of P2 (large alveolus on right and fragmentary dentine on left), there is no trace of P1, nor is there sufficient space within the tooth row to have accommodated this tooth. It is thus reasonable to conclude that P1 is completely lost in INT B. While this taxon has fairly clearly lost an anterior tooth, its precise identity is open to multiple interpretations. As just discussed, we favor the view that P1 has been lost, and that the fragmentary tooth anterior to P3 is likely P2 (on the basis of the apparent similarity of the latter two teeth). It is not inconceivable, however, that I2, I3, or C

is lost, making the slightly worn tooth anterior to the alveolus P1. This possibility seems unlikely given that P1 in adult interatheriines is usually well worn (this observation, coupled with details of premolar replacement, has contributed to the suggestion that the first premolar may be unreplaced in notoungulates [Sinclair, 1909; Hitz *et al*., 2000; Bond, pers. comm.; pers. obs.]). The fourth tooth in the dental series of INT B is little worn, suggesting that it had only recently erupted, and thus is likely not P1. If this interpretation is correct, the fourth tooth is logically the canine, with I1-3 anterior to it. Again, this suggests loss of P1 in INT B, a conclusion that remains tentative until more complete material becomes known. A more posterior premolar (or even a molar) could conceivably have been lost, but the well-preserved posterior dentition forms such a continuous series that we prefer to regard these teeth as P3-M3.

P3 is significantly larger than the incisors and canine. A deep, vertical groove divides the middle of the ectoloph, between the paracone and metacone. This groove would apparently become more subtle with wear, as it shallows toward the base of the tooth, but does not disappear entirely. A small parastyle is separated from the paracone by a narrow vertical groove (much shallower and less conspicuous than the groove between the paracone and metacone). P3 is "premolariform" in that the paraloph is poorly developed in comparison to the large metaloph, i.e., the metaloph projects much further lingually than the paraloph, and no distinct sulcus separates these structures lingually. P4 is molariform. The para- and metalophs, separated lingually by a deep vertical sulcus, are roughly the same length labiolingually, but the paraloph is slightly larger given its greater thickness mesiodistally. The occlusal surface of P4 thus forms two adjacent, u-shaped basins, the curved margins of which face lingually. The P4 paracone forms a strong column on the tooth's external face, as in *Brucemacfaddenia* and *Interatherium*, and INT C (described

herein) (note that these pronounced and columnar paracones occur on different teeth in these taxa: on P2-4 in *Brucemacfaddenia* and *Interatherium,* P3-4 in INT C, and P4 in INT B). A deep vertical groove on the ectoloph divides the paracone and the small, somewhat rounded parastyle. Posterior to paracone column, the external face bears several faint, vertical grooves.

Although progressively smaller than P4, M1-3 resemble P4 in occlusal outline; large paralophs and slightly smaller metalophs form adjacent, u-shaped basins separated lingually by a deep sulcus. An extremely thin but distinct paracone column occurs on M1. The relatively large parastyle of M1 is separated from the paracone column by a shallow groove. The external face also bears a shallow vertical groove at the metacone. The M2-M3 lack conspicuous parastyles, and their external faces bear several shallow, vertical furrows and thin columns, giving them a striated appearance.

As only the crowns of the teeth can be examined in SGOPV 5559, it is not absolutely certain that they are hypselodont. Nevertheless, three observations strongly suggest that P3-M3 are indeed hypselodont: 1) the morphology of P3-M3 most closely resembles other hypselodont interatheriines; 2) the specimen's age (~19.5 Ma) corresponds to a time when only hypselodont interatheriines are known; and 3) interatheriines with hypsodont but not hypselodont cheek teeth (e.g. *Santiagorothia*, *Eopachyrucos*, *Proargyrohyrax*) are often characterized by posterior premolars and molars with anteroexternal and posteroexternal fossettes in early wear stages, and lingual fossettes with moderate to advanced wear (see e.g., Hitz *et al*., 2000) – in SGOPV 5559 P3-M3 lack such fossettes.

Interatheriidae gen. *et* sp. *nov*. C

Fig. 2.5, table 2.3

HOLOTYPE: SGOPV 3210, a left maxillary fragment bearing P2-M3.

PARATYPE: SGOPV 3974, a left upper tooth row, with complete C-P1, nearly complete P2-4 (these teeth have small chips along the ectoloph), and partial M1-3 (the labial portions of which are not preserved). No additional material is referred to this taxon.

DISTRIBUTION AND AGE: This taxon is known from two localities, ~300 km apart, in the Andes of central Chile. The holotype (SGOPV 3210) was recovered from a talus block at the base of steep exposures of the Abanico Formation, along the southern flank of Río Las Leñas (~100 km south-southeast of Santiago, and ~300 km north-northeast of LdL). This specimen was collected from the same large, volcaniclastic, city-bus-sized boulder that yielded the holotype of *Chilecebus carrascoensis* (SGOPV 3213) (Flynn *et al*., 1995). An $^{40}Ar/^{39}Ar$ date from the same boulder indicates an age of 20.09 ± 0.27 Ma.
SGOPV 3974 was collected at locality C-04-36, ~6 km north of LdL, from an outcrop of the Cura-Mallín Formation (CMF) exposed along the western slopes of the northermost tributary of LdL. By contrast, most fossils from the LdL region have been recovered from localities *south* of the lake. Although locality C-04-36 occurs within exposures mapped as CMF (Niemeyer and Muñoz, 1983), these units have not been correlated in detail to the subdivisions of the CMF ($T_{CM1-5}$) mapped south of LdL (Herriot, 2006; Flynn *et al*., 2008). It is notable, however, that SGOPV 3210, which is conspecific with SGOPV 3974, has been dated to ~20 Ma – consistent with the older end of the known age range of the CMF near LdL.

DIAGNOSIS: The diagnosis of Interatheriinae gen. *et* sp. *nov*. C (informally referred to as INT C) is necessarily limited to C-M3 (fig. 2.5). Derived characters distinguishing INT C from more basal, pre-Deseadan interatheriines (e.g., *Eopachyrucos*, *Proargyrohyrax*, and *Santiagorothia*; see figs. 2.9-11 for phylogenetic analysis) include hypselodont molars and premolars (see discussion in description below), and cheek teeth that maintain a persistent lingual sulcus, but lose all traces of the anteroexternal and posteroexternal fossettes with wear. The upper canine of INT C is "robust" (labiolingually wide) and subequal in size to P1. A similarly robust canine occurs in many early-diverging interatheres (e.g., *Notopithecus*, *Plagiarthus*, *Santiagorothia*, and *Brucemacfaddenia*), contrasting with the relatively slender canine in *Ignigena* and many Deseadan and younger taxa, including *Cochilius*, *Federicoanaya*, *Miocochilius*, and *Protypotherium* (this character is variable in *Protypotherium*).

INT C possesses a premolariform P2 but molariform P3-4. A similar pattern of molarization characterizes *Cochilius*, *Plagiarthus*, and *Santiagorothia*. INT C differs from both *Cochilius* and *Plagiarthus* in having a relatively "robust" P2-M1 (that is, these teeth are relatively wider labiolingually in INT C). This difference is particularly striking in P3-4, which in INT C are nearly as wide (labiolingually) as they are long (mesiodistally). Compared to *Cochilius*, INT C also has a more robust canine (see above) and a larger P4 paraloph (in INT C the P4 paraloph and metaloph are subequal in size, whereas in *Cochilius* the P4 paraloph is notably smaller than the metaloph). INT C is further distinguished from *Plagiarthus* by the shape of P2; in INT C it is roughly triangular in outline and bears a faint lingual sulcus, whereas in *Plagiarthus* it is more quadrangular and lacks any trace of a lingual sulcus.

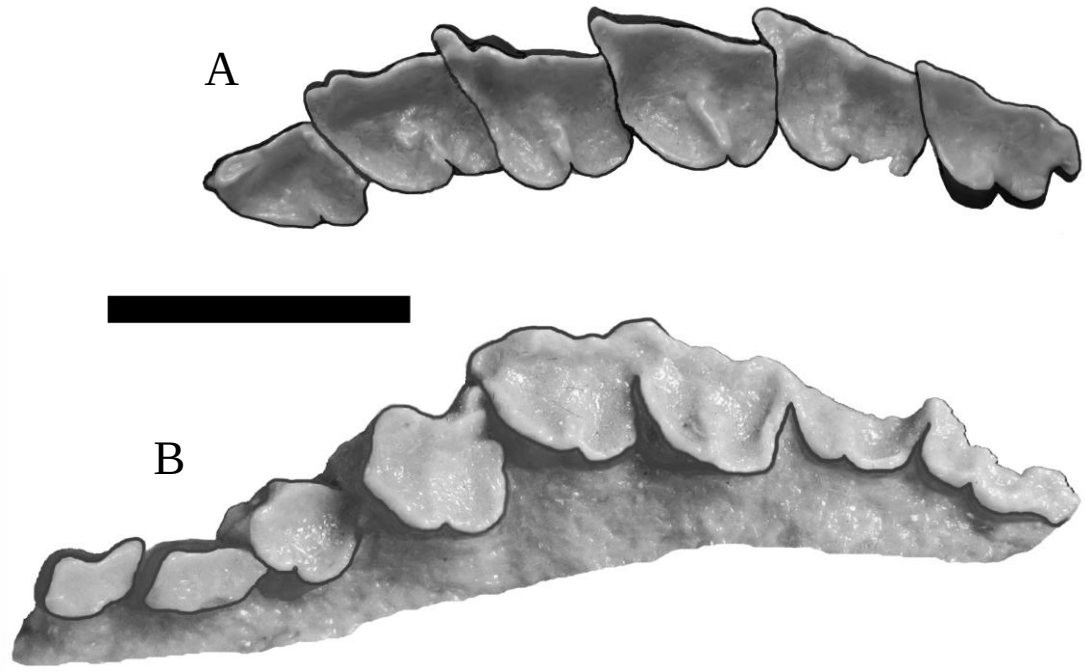


FIGURE 2.5. Dentitions of Interatheriinae gen. *et* sp. *nov*. C. **A**: Holotype SGOPV 3210, left P2-M3 in occlusal view, recovered along the southern flank of Río Las Leñas (~100 km south-southeast of Santiago, and ~300 km north-northeast of LdL); **B**: Paratype SGOPV 3974, left C-M3 (but note that anterolabial margins of P2-3 and labial margins of P4-M3 are broken), recovered from an outcrop of the Cura-Mallín Formation ~6km north of Laguna del Laja. Sclae bar = 1 cm.

**TABLE 2.3: Dental measurements (mm) for upper dentition of INT C.**

MD = mesiodistal; LL = labiolingual

| Tooth | SGOPV 3210 | SGOPV 3974 |
|---|---|---|
| C MD | | 3.88 |
| C LL | | 2.14 |
| P1 MD | | 4.18 |
| P1 LL | | 2.1 |
| P2 MD | 4.75 | 4.6* |
| P2 LL | 3.77 | 3.5* |
| P3 MD | 5.41 | 5.1* |
| P3 LL | 4.65 | 4.3* |
| P4 MD | 6.09 | 5.9* |
| P4 LL | 5.14 | 4.6* |
| M1 MD | 6.42 | |
| M1 LL | 4.62 | |
| M2 MD | 6.26 | |
| M2 LL | 4.21 | |
| M3 MD | 5.84 | |
| M3 LL | 3.46 | |

*measurement approximate.

Beyond sharing molarized premolars, INT C and *Santiagorothia* have labiolingually wide premolars and M1. Among interatheriines, a wide M1 also characterizes *Proargyrohyrax*; in both *Proargyrohyrax* and *Santiagorothia* M1-2 become more equidimensional with wear (note that in INT C, the relative length/width ratio of M2 is difficult to determine since in SGOPV 3210 and SGOPV 3974 this tooth is either distorted or fragmentary). INT C is distinguished from *Santiagorothia* and *Proargyrohyrax* by the following features in INT C: hypselodont cheek teeth (*Santiagorothia* and *Proargyrohyrax* are hypsodont; hypselodonty in INT C is described more fully below); cheek teeth lack any trace of anteroexternal, posteroexternal, or lingual fossettes (in *Santiagorothia* and *Proargyrohyrax* the former two fossettes occur in early to moderate wear stages, while the latter fossette develops in moderate to advanced wear stages); and smaller size (SGOPV 3210, the larger of the two specimens known, is smaller than all adult specimens of *Santiagorothia* and *Proargyrohyrax.* In fact, the teeth of SGOPV 3210 are similar in size to those in SGOPV 2827 – a small specimen of *Santiagorothia* with unworn molars and deciduous premolars).

DESCRIPTION: The C-M3 of INT C (fig. 2.5) are similar in dimensions to their counterparts in medium-sized interatheriines such as *Brucemacfaddenia*, *Protypotherium*, *Cochilius*, INT A, and INT B. Among other well-known interatheres, the teeth of INT C are larger than in *Federicoanaya* and *Interatherium*, but smaller than in *Santiagorothia* and *Miocochilius.*

The canine and P1 are similar in size and shape – roughly quadrangular in occlusal outline, with a distinct anteroexternal ridge along the labial margin (this ridge is more pronounced in the canine than P1). P2 is much broader labiolingually than C-P1, and in

occlusal outline it is narrow anteriorly and broad posteriorly, giving this tooth a roughly triangular form. P2 is "premolariform" in that the paraloph is significantly less developed than the metaloph; these lophs are separated lingually by a sulcus that appears to persist with wear. The paracone forms a vertical ridge along the exterior surface of the tooth, and is separated from a small parastyle by a vertical groove. In all these respects, the P2 of INT C closely resembles P2-4 of *Protypotherium*.

P3-4 are "molarifom," possessing a well-developed protoloph and metaloph (both u-shaped) that are separated lingually by a distinct sulcus. As such, P3-M3 are generally similar, except as noted below. P3-M2 are relatively wide labiolingually (M3, as in most interatheres, is the narrowest tooth); P3-4 are particularly robust, being nearly as wide (labiolingually) as they are long (mesiodistally). On P3-4 the paracone forms a distinct, vertical ridge along the labial face; the paracone is separated from the parastyle by a deep vertical groove. In contrast, on M1-3 the labial surface is relatively smooth (lacking a distinct paracone ridge), and the groove between the paracone and parastyle is either vague or absent. On P3 and M1-2 the lingual margin of the paraloph bends posteriorly. The P4 paraloph lacks this bend, but it is notable for its large size (see diagnosis). M3 bears a narrow, posteriorly projecting metastyle. In both SGOPV 3210 and SGOPV 3973, breakage has exposed the extremely long roots of several molars and premolars. These roots do not taper toward their bases (as in *Santiagorothia*), indicating that these cheek teeth were hypselodont.

*Protypotherium* Ameghino, 1887b

SYNONYMY: *Toxodontophanus*, Moreno, 1882, pg. 23 (*nomen nudum*); Ameghino, 1887a, pg. 64

*Patriarchus*, Ameghino, 1889, pgs. 480-481; Ameghino, 1891b; Ameghino 1894

TYPE SPECIES: *Protypotherium australe*, Ameghino 1887b (but see discussion in Remarks, taxonomic note 1)

DISTRIBUTION AND AGE: The best known and most abundant collections of *Protypotherium* have been recovered from the Santa Cruz Formation in Argentine Patagonia (Santacrucian SALMA; late early Miocene) (e.g., Moreno, 1882; C. Ameghino, 1890; F. Ameghino, 1887b, 1889, 1891, 1894; Hatcher, 1903; Scott, 1928; Sinclair, 1909; Lane, 1927; Tauber 1996, 1997). Santacrucian or "Pinturan"-aged fossils of *Protypotherium* have also been reported from the southern Chilean Andes, just east of Pampa Castillo (Flynn *et al*., 2002), as well as from the Lonquimay basin in the central Chilean Andes (Suarez *et al*., 1990; Buldrini and Bostelmann, 2011). Herein we report three specimens of *Protypotherium praeuritulum* from near Laguna del Laja.

*Protypotherium* has also been reported from the Colhuehuapian of Argentina (Bordas, 1939; Barrio *et al*., 1986; Kramarz *et al*., 2005), and "Pinturan" levels at the Gran Barranca, Argentina (Kramarz *et al.*, 2010), but the evidence for at least some of these early occurrences is inconclusive (in fact, specimens described by Bordas [1939] are certainly not assignable to *Protypotherium*; see Remarks below, and appendix 2.4). Post-Santacrucian records include those from the Friasian in Argentina (Roth, 1920; Kraglievich, 1930); the Colloncuran in Argentine Patagonia (Rolleri *et al*., 1948; Bondesio *et al*., 19080a); the

Chasicoan in Buenos Aires province, Argentina (Cabrera and Kraglievich, 1931; Bond and López, 1996; Bondesio *et al*., 1980b); the Chasicoan in Venezuela (Linares, 2004); the "Conglomerado osífero" of the Ituzaingó Formation, Entre Ríos Province, Argentina (Ameghino 1885; this unit may correspond temporally to the Huayquerian SALMA [Cione *et al*., 2000]); and the late Miocene (likely Huayquerian SALMA) of La Rioja Province, Argentina (Tauber, 2005). The prelimiarny taxonomic assessment presented herein suggests that some of these occurences require reconsideration.

EMENDED DIAGNOSIS: *Protypotherium* is easily distinguished from the earliest diverging interatheriines (*Eopachyrucos, Proargyrohyrax,* and *Santiagorothia*; see figs. 2.9-11 for our phylogenetic analysis) by possessing hypselodont molars and premolars, as well as upper molars and premolars with persistent lingual sulci, but antero- and posteroexternal sulci that are lost early in wear. *Protypotherium* is further derived with respect to *Plagiarthus* and *Brucemacfaddenia* (in addition to *Eopachyrucos, Proargyrohyrax,* and *Santiagorothia*) in possessing more procumbent lower incisors, and lacking a persistent lingual sulcus and distinct metacristid on the lower molar trigonids.

The upper premolars of *Protypotherium* are "non-molarifom" – that is, the paralophs of P2-4 are significantly less developed than the metalophs (although P1 is also non-molariform, it is generally ovoid and lacks distinct lophs altogether). This premolar morphology differs markedly from that of most other hypselodont interatheriines in that P3-4 are "molariform" in *Plagiarthus*, *Brucemacfaddenia*, INT C, *Archaeophylus*, *Interatherium*, and *Cochilius*; P2 is also molariform in *Archaeophylus*, *Interatherium*, and *Brucemacfaddenia*. INT B approaches the condition of *Protypotherium* (both possess non-molariform P1-3), but the P4 of INT B differs in being molariform. In possessing *all* non-molariform upper premolars, *Protypotherium* is similar to *Miocochilius* and *Federicoanaya*.

*Protypotherium* differs from *Miocochilius* and *Federicoanaya* in possessing an m1 talonid that is larger than the trigonid (in *Miocochilius* and *Federicoanaya* the talonid is subequal to or smaller than the trigonid); m2-3 talonids that are sub-triangular with narrow anterior margins (they are quadrangular in *Federicoanaya* and semi-circular in *Miocochilius*); and notably smaller P2-4 parastyles. *Protypotherium* is further distinguished from *Miocochilius* by having a more closed dental series (while some specimens of *Protypotherium* have small gaps between the anterior teeth, these do not approach the diastemata between I3-C and c-p2 in *Miocochilius*); a relatively large p1 that is similar in size to p2 (in *Miocochilius* p1 is notably smaller than p2); and a salient lingual sulcus on the m3 talonid (whereas in *Miocochilius* the m3 talonid has a salient labial sulcus).

In the phylogenetic analysis presented below (see figs. 2.9-11), *Protypotherium* and INT A are resolved as sister-taxa, which in turn form a clade with *Progaleopithecus* and *Miocochilius*. *Progaleopithecus* and INT A, known primarily from lower dentitions, share several derived features with *Protypotherium*, including columnar i1-2 (in *Protypotherium* and *Progaleopithecus*, these teeth are bicolumnar in early wear stages; it is unknown if this was also characteristic of INT A) and sub-triangular m2-3 trigonids with narrow anterior margins. *Protypotherium*, *Progaleopithecus*, and INT A also possess a salient lingual sulcus on the m3 trigonid (although this feature is infrequently subdued in *Protypotherium*); *Progaleopithecus*, however, also bears a salient labial sulcus on the m3 trigonid (*opposite* the lingual sulcus), which is absent in *Protypotherium*. *Protypotherium* is readily distinguished from both INT A and *Progaleopithecus* by its lower premolars: in *Protypotherium*, the p2-4 talonids are significantly smaller than their respective trigonids (as in *Miocochilius* and *Federicoanaya*), whereas in INT A and *Progaleopithecus* the p2-4 talonids are subequal to or larger than the trigonids.

REMARKS: A thorough description of the cranial and postcranial morphology of *Protypotherium*, and its diagnosis, is provided by Sinclair (1909). The preceding diagnosis is limited to the dentition, intended to clarify lingering taxonomic problems, and to distinguish *Protypotherium* from several recently described interatheriines (see Hitz *et al*., 2000, 2008; Reguero *et al*., 2003; this study), which are primarily known from dentitions.

Florentino Ameghino described this genus in 1885, on the basis of a fragmentary mandibular symphysis (collected by Pedro Scalibrini) and a partial right mandible bearing p4-m3 (collected by Santiago Roth). These specimens were recovered from the riverside cliffs of the Río Paraná, near the city of Paraná (the age and stratigraphic correlations of the source beds – the "Conglomerado osífero" of the Ituzaingó Formation [late Miocene] – are discussed by Cione *et al*. [2000]). These mandibular fragments were identified as a new species, *Protypotherium antiquum* (Ameghino, 1885; this taxon is further described in Ameghino, 1887a, 1889), although this name also appears in an earlier list without any description (Ameghino, 1882).

*Protypotherium* is best known from the Santa Cruz Formation (Santacrucian SALMA; late early Miocene). The Patagonian expeditions of Francisco Moreno (expedition in 1877) and Carlos Ameghino (first expedition in 1887) produced extensive collections of fossils from the valleys and banks of the Río Santa Cruz (see Moreno, 1882; C. Ameghino, 1890, 1891; F. Ameghino, 1891), and resulted in the description of several new species of *Protypotherium*. Based on these collections, Florentino Amegino (1887b) recognized three additional species in this genus: *P. australe* (originally listed as *Toxodontophanus australis* by Moreno [1882] [*nomen nudum*]), *P. praerutilum*, and *P. attenuatum*. Ameghino's original description of these taxa was brief (Ameghino, 1887b), and the following year Ameghino (1888) provided another short description of a new species, *P. obstructum*, from Monte

Hermoso (Araucana Formation, "Piso Hermosico," 60 km from Bahia Blanca). In 1889, Ameghino more thoroughly described these five taxa, and introduced two new ones – *P. claudum* and *Patriarchus palmidens*, both based on specimens collected during Carlos Ameghino's first Patagonian expedition (Ameghino, 1889) (note that Sinclair [1909] synonymized *Patriarchus* with *Protypotherium*). Further examination of these Patagonian specimens led Ameghino to describe several additional species: *Protypotherium globosum*, *P. convexidens*, *P. diversidens*, *P. compressidens*, *Patriarchus furculosus*, *P. distortus*, *P. rectus*, *P. diastematus*, *P. leptocephalus*, and *P. altus* (Ameghino, 1891); and later *Protypotherium lineare* and *Patriarchus icochiloides* (Ameghino, 1894; note that in this same publication Ameghino reassigned *Patriarchus distortus* as *Protypotherium distortum*).

Under the auspices of Princeton University, John Bell Hatcher led a three-stage expedition to Patagonia from 1896-1899. These campaigns resulted in abundant and subsequently well-studied collections of fossil mammals, primarily from exposures of the Santa Cruz Formation along the mouth of Río Gallegos and up the coast to Santa Cruz, and inland reaching as far as Lago Belgrano and Lago Pueyrredón (see Hatcher, 1903; Scott, 1928; Marshall, 1976). Largely on the basis of these collections, Sinclair (1909) thoroughly revised *Protypotherium*, synonymizing nearly all the species within *Patriarchus* and *Protypotherium* with either *Protypotherium australe*, *P. praerutilum*, or *P. attenuatum* (although Sinclair listed *P. diversidens*, *P. diastematum*, and *P. claudum* as Typotheria *incertae sedis*, and *P. obstructum* was not discussed).

Subsequent works have introduced new species to the genus. Based on a single specimen from the Santa Cruz beds near Río Gallegos, Lane (1927) described *P. martini*. Cabrera and Kraglievich (1931) described two additional taxa, *P. distinctum* and *P. minutum*, on the basis of specimens collected from the Arroyo Chasicó Formation in Buenos

Aires province. Finally, Bordas (1939) described *P. minor* from among the Colhuehuapian-aged fossils collected along the southern banks of the Río Chubut, near the city of Gaiman (see below, table 2.4, and appendix 2.4 for further discussion of these taxa).

More recently, several authors have offered brief remarks with regard to *Protypotherium* (Bond and López, 1996; Kramarz *et al*., 2005; Tauber, 2005; Krapovickas *et al*., 2008; Krapovickas, 2009; Buldrini and Bostelman, 2011), but Tauber (1996) provided the most detailed recent treatment of the genus. Tauber's (1996) work relied on abundant new collections of *Protypotherium* from coastal exposures of the Santa Cruz Formation between Río Coyle and Río Gallegos, not only resulting in a partial revision of the genus, but also contributing to a more detailed understanding of the biostratigraphic ranges of *P. australe, P. praerutilum*, and *P. attenuatum* (see also Tauber, 1997).

The aforementioned publications (among others) pertaining to the taxonomy of *Protypotherium*, together with an extensive firsthand examination of relevant museum collections, highlight several problematic issues. In lieu of a thorough taxonomic revision of this taxon – long overdue but beyond the scope of this work – we offer the following preliminary remarks:

1. Strict priority dictates that the type species of *Protypotherium* is *P. antiquum* Ameghino, 1885. Although the priority of *P. antiquum* is acknowledged in some studies (e.g., Bond and López, 1996; Cione *et al*., 2000; Kramarz *et al*., 2005; Buldrini and Bostelmann, 2011), others cite Ameghino, 1887b (in which *P. australe, P. praerutilum*, and *P. attenuatum* are described) as the original description of the genus (e.g., Sinclair, 1909; Tauber, 1996). Certainly, the three species described by Ameghino in 1887b are much better known than *P. antiquum* Ameghino, 1885. The

latter taxon was described on the basis of two mandibular fragments, only one of which possesses teeth (Ameghino, 1885). A cast of these teeth (MACN-A 1288; p4-m3) was examined at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia." The original specimen (ZMUC ZMK 21/1877) is housed at the Zoological Museum – University of Copenhagen. There are certainly similarities between this specimen and the dentitions of the well-known species of *Protypotherium* (*P. australe*, *P. praerutilum*, and *P. attenuatum*). Still, one significant difference exists: the m3 of ZMUC ZMK 21/1877 bears a very deep and distinct *labial* sulcus, as well as a less pronounced *lingual* sulcus. In all other specimens of *Protypotherium* examined in this study, a distinct *lingual* sulcus is almost invariably present, but a pronounced *labial* sulcus is not observed (however, we note that a very subtle and broad labial groove is variably present: e.g., this character has been considered diagnostic of *P. minutum* [see Bond and Lopez, 1996], and is evident in MACN-A 3884 [*P. australe*]). This observation informs our diagnosis of *Protypotherium*, as we emphasize the absence of a strong labial sulcus on m3 (see Emended Diagnosis above). Accordingly, ZMUC ZMK 21/1877 (holotype of "*P. antiquum*") possesses characters that would seem to preclude its inclusion within *Protypotherium*, as commonly applied and according to the diagnosis presented here. While it is conceivable that a broader diagnosis of the genus would recognize the validity of *P. antiquum*, we argue against this course of action for four primary reasons. 1) The hypodigm of "*P. antiquum"* is not informative. Evidently only two specimens have been assigned to this taxon – one a mandibular symphysis that has not been located, and the other (ZMUC ZMK 21/1877) only possesses p4-m3. 2) Although the p4 of ZMUC ZMK 21/1877 is most

similar to *Protypotherium* among known interatheriines, especially in that the talonid is highly reduced and abuts closely against the trigonid, a p4 approaching this morphology occurs elsewhere (*Miocochilius*, *Federicoanaya*). 3) The m1-m2 of ZMUC ZMK 21/1877 bear little diagnostic information. 4) The strong lingual sulcus on the m3 of ZMUC ZMK 21/1877 is more similar to *Miocochilius* and *Progaleopithecus* than it is to *Protypotherium*. As such, we suggest that the taxon "*Protypotherium antiquum*" is of dubious validity, and regard ZMUC ZMK 21/1877 as Interatheriinae *incertae sedis.* This decision is admittedly complicated by the fact that the first description of *Protypotherium* was of *P. antiquum* (Ameghino, 1885), and that the second taxon included in this genus, *P. australe*, was initially identified as *Toxodontophanus australis* (*nomen nudum* in Moreno, 1882; brief description in Ameghino, 1887a). Still, shortly thereafter, Ameghino (1887b) reassigned this taxon to *Protypotherium*, and *P. australe* has become known from abundant material and referred to ubiquitously in the literature for more than a century. The name *Toxodontophanus*, on the other hand, has not been recognized at valid since 1887. For this reason, we regard *Protypotherium australe* Ameghino 1887b as the genotype of *Protypotherium*, while recognizing that 1) strict priority belongs to the problematic taxon *P. antiquum* Ameghino 1885*;* and 2) *P. australe* was initially described as *Toxodontophanus australis* (*nomen nudum* in Moreno, 1882; brief description in Ameghino, 1887a).

2. What specimens constitute the holotyes of some species of *Protypotherium* is uncertain. This is partly due to the fact that Ameghino's (1885, 1887a, 1887b, 1888, 1889, 1891, 1894) original descriptions invariably lacked specimen numbers. In addition, when Ameghino left the Museo de La Plata in 1888, he was denied access

to the museum's collections (even though he described a large number of its specimens). After 1902, however, when Ameghino became director of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN) in Buenos Aires, many of the specimens to which he was supposedly denied access were housed at MACN (see Fernicola, 2011 for summary). As a result, it is often unclear whether Ameghino transferred type specimens from La Plata to Buenos Aires, or if instead he used subsequent collections to designate new types for previously described species (Fernicola, 2011; Alejandro Kramarz, personal communication; Luna, personal observation). (See table 2.4 and appendix 2.4 for identification of type specimens and/or description of pertinent material.)

3. Although we agree with Sinclair (1909) that many species of *Protypotherium* and *Patriarchus* described by Ameghino (1888, 1889, 1991, 1894) should be synonymized with *P. australe*, *P. praerutilum*, or *P. attenuatum*, we suggest that further revisions are necessary (e.g., *Protypotherium convexidens* should be considered a *nomen nudum*; *Protypotherium compressidens* may be a valid taxon; *Patriarchus rectus* should be synonymized with *Protypotherium praerutilum* instead *of P. attenuatum*; see table 2.4 and appendix 2.4). Furthermore, we question the validity of some of the diagnostic characters proposed by Sinclair (1909). For example, with respect to *P. praerutilum*, Sinclair (1909, pg. 40) asserts that, "the only positive character of specific value seems to be the narrowness of the superior molars in proportion to their length. Although the length antero-posteriorly may be the same as in some of the smaller individuals of *P. australe*, the width is always less." Our data suggest that the length/width ratios of the upper molars is actually similarly variable in both species, and thus of no diagnostic value (see Emended

Diagnosis of *P. praerutilium* below, the remarks that follow the diagnosis, and table 2.6).

4. *Protypotherium martini* was diagnosed primarily on the basis of three characters: a relatively narrow M1 (mesiodistal width/labiolingual length = 0.56); relatively wide P2-4 (mesiodistal widths/labiolingual lengths = 1, 1.25, 1.11, respectively); and premolars with a distinctly acute posterointernal margin (Lane, 1927). In other respects, the taxon is described as similar in size and morphology to *P. australe*. We make five observations: 1) Lane only had four specimens of *P. australe* available for comparison. 2) Based on a photograph of *P. martini* (Plate 26-B in Lane, 1927), our measured ratio for the mesiodistal width/labiolingual length of M1 is 0.61 (as opposed to the value of 0.56 provided by Lane [1927]). 3) We measured this same ratio for 33 specimens of *P. australe*; the values ranged from 0.55-0.71, with an average of 0.64. Therefore, even Lane's (1927) measurement falls within the range of variation observed for *P. australe*. 4) Although we did not measure the premolars of *P. australe*, we observed a wide range in premolar mesiodistal widths for this taxon. In particular, MACN-A 4001 approaches the proportions discussed by Lane (1927). 5) An acute posterointernal margin on P2-4 was also observed to varying degrees among several specimens of *P. australe* (e.g., MACN-A 3882; MACN-A 4001). Based on these observations, we suggest synonymizing *P. martini* with *P. australe.*
5. While we have not examined material of *P. distinctum* or *P. minutum* firsthand, we note that several characters identified as diagnostic for these taxa (Cabrera and Kraglievich, 1931; Bond and Lopez, 1996) may also be variably present among specimens of *P. australe*, *P. praerutilum*, and/or *P. attenuatum.*

6. *P. minor* has molariform premolars, with strongly developed paralophs that are similar in size to the metalophs, giving the occlusal surface of the premolars a generally rectangular outline. This is incompatible with any diagnosis of *Protypotherium* (e.g., Ameghino, 1889; Sinclair, 1909; herein), since the genus is characterized by premolars that are sub-triangular in occlusal outline, with relatively small paralophs. We suggest that MACN 11742 (the holotype and only specimen of "*P. minor*") be considered Interatheriinae *incertae sedis*, cf. *Interatherium*.
7. Tauber's (1996) emended diagnoses of *P. australe*, *P. praerutilum*, and *P. attenuatum* include several characters that we consider variable within each taxon and/or difficult to objectively interpret, and therefore of doubtful diagnostic value (see the emended diagnosis of *P. praerutilium*, and the remarks that follow the diagnosis).

These aforementioned taxonomic considerations suggest that a more complete revision is required, especially one focusing on the temporal range and geographic occurrences of *Protypotherium* and its constituent species. For example, although *Protypotherium* has long been recognized from the Colhuehuapian (Bordas, 1939; Kramarz *et al*., 2005), we find evidence of this early occurrence far from conclusive.

**TABLE 2.4. Taxonomic summary of *Protypotherium*.**

| Taxon | Type Material | Taxon Status | Original Description |
|---|---|---|---|
| *Protypotherium antiquum* | ZMUC ZMK 21/1877 | Interatheriinae *incertae sedis* | Ameghino, 1885 |
| ***Protypotherium australe*** | MACN-A 530, 550*†‡<br>MACN-A 3882, 3883, 3884* | **valid - type species** | Ameghino, 1887b |
| *Protypotherium claudum* | MACN-A 551‡ | junior synonym of *Protypotherium australe* | Ameghino, 1889 |
| *Patriarchus palmidens* | MACN-A 37* | junior synonym of *Protypotherium australe* | Ameghino, 1889 |
| *Patriarchus furculosus* | MACN-A 3970, 3972* | junior synonym of *Protypotherium australe* | Ameghino, 1891 |
| *Patriarchus distortus* | unknown | junior synonym of *Protypotherium australe* | Ameghino, 1891 |
| *Patriarchus altus* | MACNA-A 3999, 4000, 4001 | junior synonym of *Protypotherium australe* | Ameghino, 1891 |
| *Protypotherium lineare* | MACN-A 4038, 4039* | junior synonym of *Protypotherium australe* | Ameghino, 1894 |
| *Protypotherium martini* | KUPV 19 | junior synonym of *Protypotherium australe* | Lane, 1927 |
| ***Protypotherium praerutilum*** | MACN-A 1081,1082*‡<br>MACN-A 1083* | **valid** | Ameghino, 1887b |
| *Patriarchus rectus* | MACN-A 4005, 4006, 4007* | junior synonym of *Protypotherium praerutilum* | Ameghino, 1891 |
| *Patriarchus leptocephalus* | MACN-A 3989<br>MACN-A 3990, 3991* | junior synonym of *Protypotherium praerutilum* | Ameghino, 1891 |
| ***Protypotherium attenuatum*** | MACN-A 524*‡<br>MACN-A 627*†‡ | **valid** | Ameghino, 1887b |
| *Protypotherium globosum* | MACN-A 4049 | junior synonym of *Protypotherium attenuatum* | Ameghino, 1891 |
| *Patriarchus icochiloides* | MACNA-4021, 4022* | junior synonym of *Protypotherium attenuatum* | Ameghino, 1894 |
| ***Protyptherium compressidens*** | MACN-A 4029, 4030 | **valid** | Ameghino, 1891 |
| *Protypotherium obstructum* | MACN-A 1677 | Interatheriinae *incertae sedis* | Ameghino, 1888 |
| *Protypotherium diversidens* | MACN-A 4052 | Interatheriinae *incertae sedis* | Ameghino, 1891 |
| *Protypotheirum convexidens* | unknown | *nomen nudum* | Ameghino, 1891 |
| *Patriarchus diastematus* | MACN-A 4044 | uncertain, see appendix 3 | Ameghino, 1891 |
| *Protypotherium distinctum* | MLP 12-2178† | uncertain, see appendix 3 | Cabrera and Kraglievich, 1931 |
| *Protypotherium minutum* | MLP 12-2176, 12-2177† | uncertain, see appendix 3 | Cabrera and Kraglievich, 1931 |
| *Protyptherium minor* | MACN 11742 | Interatheriinae *incertae sedis* | Bordas, 1939 |

* correspondence to original type uncertain, see appendix 2.4 for further details
† material not examined in this study
‡ illustrated in Ameghino, 1889

*Protypotherium praerutilum* Ameghino, 1887b

SYNONYMY: *Patriarchus rectus* Ameghino, 1891
*Patriarchus leptocephalus* Ameghino, 1891

TYPE: MACN-A 1081, partial skull bearing left I1-M3 (fragmentary M1-2) and right P1-M3 (fragmentary P2, M1). MACN-A 1082, partial mandible bearing right i1-m3 and fragments of left i1-3. MACN-A 1083, partial left mandible bearing m1-3. The likelihood that all these specimens pertain to the same individual is high. See appendix 2.4 for further discussion of type material.

NEWLY REFERRED MATERIAL: SGOPV 3826, partial skull (with well-preserved right maxilla, and fragmentary left and right nasals, frontals, and parietals) bearing right I2-M3 (although the left dentition and much of the left side of the skull may still be encased in matrix). SGOPV 3835, partial skull, almost entirely encased in matrix, except for right I3-M3 and left I1-M3 (left I2-3 and left P4-M3 fragmentary). SGOPV 3941, left maxilla and zygomatic arch, and left I1-M3 (right I1-2 are also exposed, and more of the right dentition may be encased in matrix). SGOPV 5230, partial right mandible bearing p2-m3 (portions of m2-3 broken). These dentitions are shown in fig. 2.6.

DISTRIBUTION AND AGE: *Protypotherium praerutilum* is best known from the Santa Cruz Formation in Argentine Patagonia (Santacrucian SALMA; late early Miocene) (e.g., Ameghino, 1887b, 1889, Sinclair, 1909; Tauber 1996). Although the precise provenance of much of this material is unkown, Tauber's (1996, 1997) detailed biostratigraphic studies of the Santa Cruz Formation at Estancia la Costa indicate that *P. praerutilum* is widely distributed throughout this sequence (Tauber, 1996, 1997). Exposures of the Santa Cruz Formation near the Atlantic Coast are believed to span approximately 18-16 Ma (Marshall *et al*., 1986; Fleagle *et al.*, 1995; Perkins *et al*., 2012). Many specimens from older and

younger deposits and different localities have been assigned to *Protypotherium*, but these have either been assigned to different species within the genus (e.g., Ameghino, 1885, 1888; 1889; 1891; Bordas, 1939; Cabrera and Kraglievich, 1931; Bond and López, 1996), or have not been identified to the species level (e.g., Flynn *et al*., 2002; Linares, 2004; Kramarz *et al*., 2005; Tauber, 2005; Kramarz *et al*., 2010). A post-Santacrucian occurrence of *P. praerutilum* is reported from Colloncuran deposits in Argentine Patagonia, on the border of Neuquén and Río Negro provinces (Rolleri *et al*., 1948).

We recovered four specimens of *P. praerutilum* from the area south of Laguna del Laja (LdL). SGOPV 3826 (from locality C-03-5; $Tcm_3$), SGOPV 5230 (from locality C-04-17; $Tcm_3$), and SGOPV 3835 (locality C-03-7; $Tcm_1$) were recovered from Estero Trapa Trapa East, and SGOPV 3941 (locality C-04-31; $Tcm_1$) was recovered from Estero Correntoso (figs. 2.1, 2.2). SGOPV 3826 was recovered about 50 m stratigraphically below a tuff (CH 25) dated to17.70 ± 0.25 Ma and 120 m above an 8-10 m-thick ignimbrite ($Tcm_2$) dated to ~18 Ma (two different $^{40}Ar/^{39}Ar$ analyses of this ignimbrite sampled from different locations yielded ages of 17.84 ± 0.24 Ma [CH-24] and 20.0 ± 0.30 [CH-13a]) (fig. 2.2). SGOPV 3835 was recovered about 10 m stratigraphically below the ~18 Ma ignimbrite unit ($Tcm_2$), and SGOPV 5230 was recovered about 5 m stratigraphically above this ignimbrite. SGOPV 3941 was recovered from nearly the same stratigraphic position as an ash fall tuff dated to 19.8 ± 0.40 Ma [CH-11] (fig. 2.2). It should be noted, however, that the three horizons stratigraphically below the CH-11 tuff sample have yielded ages of 17.5 ± 0.40 Ma (CH-30, ~40 m below CH-11), 19.25 ± 1.0 (CH-31, ~60 m below CH-11), and 19.5 ± 0.60 (CH-32, ~170 m below CH-11) (fig. 2.2). Collectively these data suggest that specimens of *P. praerutilum* collected near LdL range in age from about 20-17.7 Ma (with some uncertainty with regard to the older limit of that range).

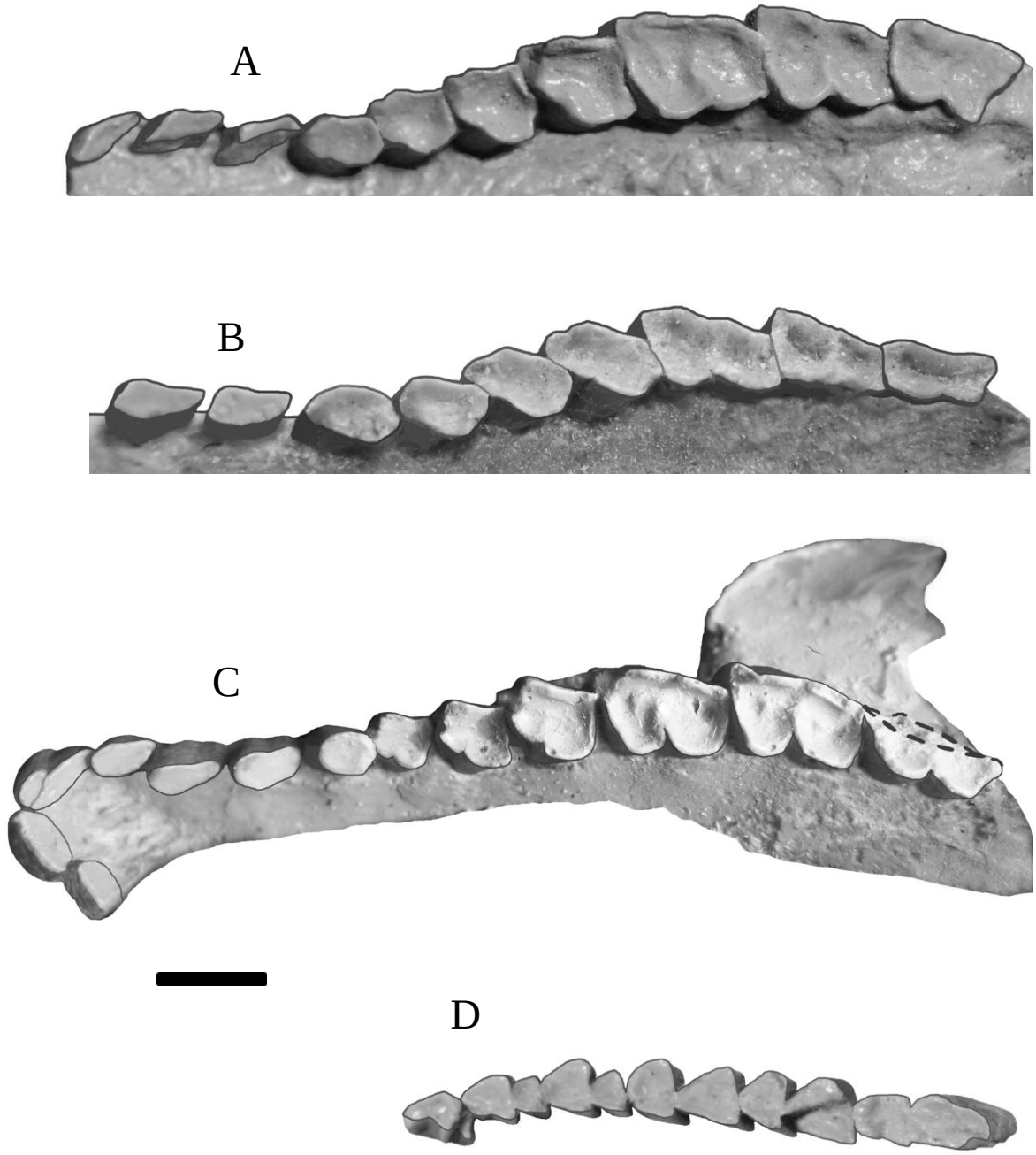


FIGURE 2.6. Dentitions of *Protypotherium praerutilum* recovered from the Laguna del Laja region. **A**: SGOPV 3826, right I2-M3 (shown as left); **B**: SGOPV 3853, right I3-M3 (shown as left). **C**: SGOPV 3941, left I1-M3 and right I1-2; **D**: SGOPV 5230, right p2-m3 (portions of m2-3 broken). Stippled lines indicate broken area of tooth. Scale bar = 0.5 cm.

EMENDED DIAGNOSIS: Typically intermediate in size between *P. australe* and *P. attenuatum* (mensural data of palate and dentition provided in tables 2.5-7, figs. 2.7-8, and appendix 2.5). Note that the teeth of the largest specimens of *P. praerutilum* are only slightly smaller than the teeth of the smallest specimens of *P. australe* (measurements based on incisors and molars; see tables 2.5, 2.6), but *P. australe* is considerably (17-42%) larger than *P. praerutilum* based on palate length (table 2.7). The relative size of I1 and I2/3 also distinguishes *P. praerutilum* and *P. australe*. The I1 of *P. praerutilum* is typically only slightly larger (mesdiodistal length) than I2/3, whereas the I1 of *P. australe* is often significantly larger (mesdiodistal length) than I2-3 (table 2.5; also, see Remarks for possible exceptions).

Although *P. praerutilum* exhibits a larger size range than *P. attenuatum*, there is considerable overlap in size between these taxa, making them difficult to distinguish on this basis alone. In fact, the size range of *P. attenuatum* actually falls *within* the lower end of the size range of *P. praerutilum* (figs. 2.7-8, tables 2.5-7). Accordingly, we suggest the following diagnostic characters: 1) upper cheek teeth of *P. praerutilum* form a series that is noticeably less curved than in *P. attenuatum*; and 2) the palate of *P. praerutilum* is relatively narrower than that of *P. attenuatum*, which is evident in a higher palate length/width ratio in *P. praerutilum* (table 2.7) (see Remarks below for further discussion of the diagnostic characters between *P. praerutium* and *P. attenuatum*, including reservations and implications). Compared to *P. compressidens* (which we consider valid; see table 2.4 and appendix 2.4), the upper molars of *P. praerutilum* are relatively wider labiolingually (table 2.6 and fig. 2.7).

**TABLE 2.5: Measurement ranges (and averages) of *Protypotherium* incisors (mesiodistal lengths in mm).** "Typical" *P. praerutilum* specimens include two specimens from LdL (SGOPV 3835 and SGOPV 3941). "Anomalous" *P. praerutilum* include MLP 26-IV-15-1 and MACN-A 9653, which have larger I1 than "typical" *P. praerutilum* specimens. See appendix 2.5 for more complete specimen information.

| Taxon | I1 size range (average) | I2 size range (average) | I1/I2 ratio range (average) | I3 size range (average) | I1/I3 ratio range (average) |
|---|---|---|---|---|---|
| *P. australe* (n=15) | 5.70-7.10 (6.40) | 4.50-5.50 (5.04) | 1.14-1.40 (1.27) | 4.53-5.40 (4.98) | 1.14-1.43 (1.29) |
| "typical" *P. praerutilum* (n=7) | 3.70-4.50 (4.01) | 3.2-4.2 (3.69) | 1.04-1.15 (1.09) | 3.50-4.30 (3.78) | 1.03-1.11 (1.07) |
| "anomolous" *P. praerutilum* (n=2) | 5.00-5.18 (5.09) | 3.66-3.72 (3.69) | 1.37-1.39 (1.38) | 3.9 (n=1) | 1.28 (n=1) |
| *P. attenuatum* (n=1) | 4 (n=1) | 3.7 (n=1) | 1.08 (n=1) | 3.68 (n=1) | 1.08 (n=1) |

**TABLE 2.6: Measurement ranges (and averages) of *Protypotherium* molars (in mm).** *P. praerutilum* includes three LdL specimens (SGOPV 3826, SGOPV 3835, and SGOPV 3941). See appendix 2.5 for more complete specimen information. Abbreviations: md = mesiodistal; ll = labiolingual.

| Taxon | M1 md range (average) | M1 ll range (average) | M1 md/ll range (average) |
|---|---|---|---|
| *P. australe* (n=34) | 8.0-9.6 (8.43) | 4.92-6.20 (5.35) | 1.40-1.81 (1.58) |
| *P. praerutilum* (n=20) | 6.05-7.40 (6.67) | 3.80-4.64 (4.29) | 1.40-1.72 (1.56) |
| *P. attenuatum* (n=5) | 5.80-6.50 (6.21) | 3.74-4.8 (4.15) | 1.33-1.64 (1.51) |
| *P. compressidens* (n=1) | 7.7 (n=1) | 3.66 (n=1) | 2.1 (n=1) |
| **Taxon** | **M2 md range (average)** | **M2 ll range (average)** | **M2 md/ll range (average)** |
| *P. australe* (n=31) | 7.1-8.8 (7.68) | 4.62-5.6 (4.96) | 1.40-1.76 (1.55) |
| *P. praerutilum* (n=21) | 5.58-6.80 (6.19) | 3.40-4.3 (3.93) | 1.41-1.76 (1.58) |
| *P. attenuatum* (n=3) | 5.60-6.00 (5.73) | 3.60-4.22 (3.90) | 1.42-1.56 (1.47) |
| *P. compressidens* (n=1) | 6.80 (n=1) | 3.40 (n=1) | 2.00 (n=1) |
| **Taxon** | **M3 md range (average)** | **M3 ll range (average)** | **M3 md/ll range (average)** |
| *P. australe* (n=29) | 6.50-8.2 (7.30) | 3.76-5.3 (4.22) | 1.43-1.90 (1.73) |
| *P. praerutilum* (n=18) | 5.36-6.80 (5.9) | 2.9-3.64 (3.24) | 1.59-2.07 (1.82) |
| *P. attenuatum* (n=2) | 5.40-60 (5.70) | 3.00-3.40 (3.20) | 1.76-1.80 (1.78) |

**TABLE 2.7: Measurement ranges (and averages) of *Protypotherium* palate (in mm).** *P. praerutilum* does not include three LdL specimens (palatal measurements unavailable ). See appendix 2.5 for more complete specimen information.

| Taxon | Palate length range (average) | Palate width range (average) | Palate length/width range (average) |
|---|---|---|---|
| *P. australe* (n=15) | 53.20-59.00 (55.12) | 20.70-24.80 (22.73) | 2.21-2.65 (2.43) |
| P. praerutilum (n=9) | 41.58-45.50 (43.83) | 17.5-19.8 (18.66) | 2.27-2.41 (2.35) |
| P. attenuatum (n=1) | 42.00 (n=1) | 20.70 (n=1) | 2.03 (n=1) |

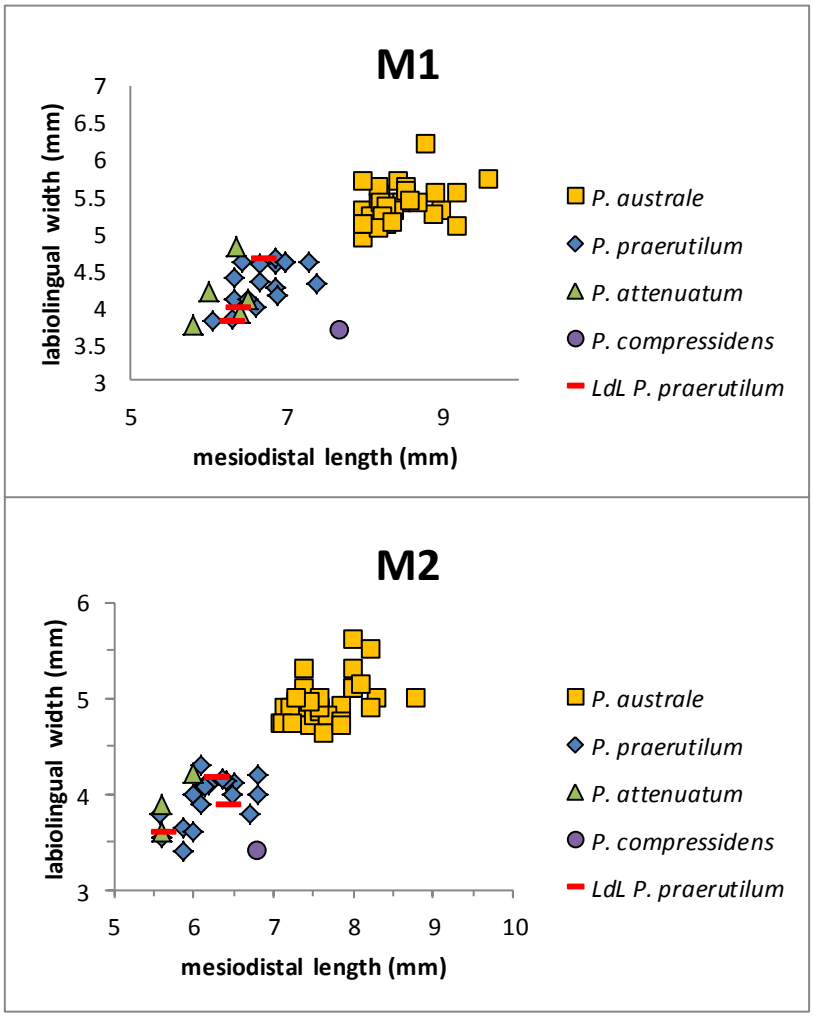


FIGURE 2.7. M1/M2 measurements of *Protypotherium* specimens. Two major size clusters are observed: *P. australe* has larger teeth, while *P. praerutilium* and *P. attenuatum* have smaller teeth that overlap in size range. Specimens from LdL fall within the size range of *P. praerutilum* (see text for additional distinctions between *P. praerutilum* and *P. attenuatum*). *P. compressidens* has very narrow M1/2, falling outside the range seen in other taxa, prompting us to recognize the validity of this taxon

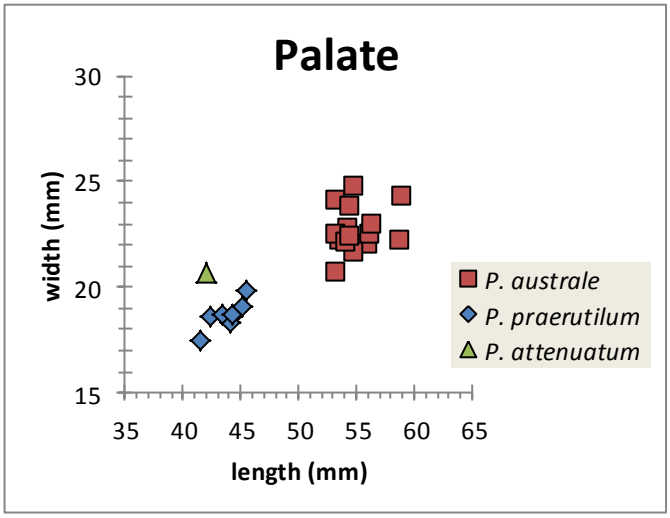


FIGURE 2.8. Palate measurements of *Protypotherium* specimens. Two major size clusters are observed: *P. australe* has a large palate compared to *P. praerutilium* and *P. attenuatum*. *P. attenuatum* has a palate length that falls within the range of *P. praerutilum*, but the palate of *P. attenuatum* is relatively wide. This difference is related to the highly curved tooth row (especially P2-4) that may be diagnostic of *P. attenuatum*.

REMARKS: Ameghino (1887b) originally described *P. praerutilum* as intermediate in size between *P. australe* and *P. attenuatum*, and further suggested that the upper dental series of *P. praerutilum* is not as highly curved as in *P. attenuatum*. Our diagnosis of *P. praerutilum* generally supports this original interpretation.

Sinclair (1909) was hesitant to recognize *P. praerutilum* as a distinct taxon, remarking that "the species as it stands now is a rather ill-defined assemblage of individuals intermediate in size between *P. attenuatum* and *P. australe*" (p. 40). We propose that the differences in size and morphology between *P. praerutilum* and *P. australe* (discussed in the above diagnosis) are certainly sufficient to recognize the validity of both taxa, but agree with Sinclair that distinguishing *P. praerutilum* and *P. attenuatum* is sometimes difficult. We note that Sinclair proposed (or at least implied) three additional diagnostic characters for *P. praerutilum*, which we consider either invalid or of dubious value. 1) The upper molars of *P. praerutilum* are relatively narrow (labiolingual width) compared to those of *P. australe*. We find, however, that the ratio of mesiodistal length/labiolingual width for the upper molars of *P. praerutilum* and *P. australe* overlap considerably (table 2.6), making this an ineffective criterion for distinguishing these taxa. 2) In his diagnosis of *P. attenuatum*, Sinclair (1909) implied that *P. praerutilum* lacks "the marked convexity of the brain-case just posterior to the fronto-parietal suture" (p. 44) that characterizes *P. attenuatum*. We suspect that this morphology varies within all species of *Protypotherium*, noting, for example, that similar concavity is observed in much larger specimens of *P. australe* (e.g., MACN-A 37). 3) Sinclair (1909) suggests that the mandible of *P. praerutilum* is a less robust than that of *P. attenuatum*. While this may be a valid distinction, this highly qualitative characteristic is difficult to apply in practice, especially given the scarcity of complete mandibles of these taxa, and thus our poor sense of their true morphological variation.

Tauber (1996) identified ten characters as diagnostic of *P. praerutilum*, a brief assessment of which is provided below (translated from Spanish):

1. **Reduced size (intermediate between *P. australe* and *P. attenuatum*):** We recognize this as a useful diagnostic character with the qualifications given in the Emended Diagnosis (above).
2. **Mesiodistal length of upper incisors reduced**: While I2-3 are smaller than those in *P. australe*, we suspect this difference merely reflects the generally smaller size of *P. praeritilum* with respect to *P. australe* (although I1 is a special case, see below). The mesiodistal length of I2-3 in *P. attenuatum* (measured from only one specimen – CORD-PV 1222) is close to the average size of I2-3 for *P. praerutilum*. See table 2.5 for mensural data of incisors.
3. **I1 with the crown scarcely curved posteriorly:** This character is intended to distinguish *P. praerutilum* from *P. australe*. While the sharp posterior curvature of I1 that is often observed in *P. australe* is not present in *P. praerutilum*, we note that this character is by no means invariably present in *P. australe*. In fact, with regard to this curvature, some specimens of *P. australe* even display a notable degree of variability between the left and right I1. (e.g., CORD-PV 1381; CORD-PV 25 [numero de campo]).
4. **Mesiodistal length of I1 approximately equal to I2 and I3:** This character is generally useful in distinguishing *P. praerutilum* and *P. australe*, since the I1 of *P. australe* is commonly significantly larger than I2 and I3 (based on mesiodistal length). We note, however, that this character varies considerably in both taxa, making this distinction far from absolute. Considering the ratio of I1/I2 (mesiodistal

length), for example, our data show a slight overlap in the ranges of these values for *P. australe* and "typical" representatives of *P. praerutium*, (although the maximum and average values for *P. australe* are much higher; see table 2.5). Moreover, we examined two specimens of *P. praerutilum* (MACN-A 9653 and MLP 26-IV-15-1; labeled as *P. praerutilum* and consistent with the size range of this taxon) that were "anomolous" in possessing relatively large first incisors, with the ratios of I1/I2 and I1/I3 (mesiodistal lengths) approaching the maximum values calculated for *P. australe* (note that these two "anomalous" specimens were included separately in table 2.5 in order to highlight generalities). Finally, we note that Buldrini and Bostelmann (2011) report a large specimen of *Protypotherium* (SGOPV 21.000; size consistent with the largest specimens of *P. australe*) with upper incisors of relatively uniform size. We have not examined this specimen, and it is unclear whether it would fall within the range of variation for *P. australe* observed in this study. These "anomalous" taxa suggest three alternative interpretations: 1) They may be truly anomalous in the sense that they do not display characters that generally distinguish *P. praerutilum* and *P. australe*; 2) they represent end-members within a range of variation that has simply not yet been observed, which would undermine the value of this diagnostic character; 3) they may represent new taxa with a unique suite of characters. Choosing between these alternatives will require further evaluation and a more complete revision.

5. **Imbrication between the incisors (greater than in *P. australe*):** Our examination suggests this character varies widely in both *P. australe* and *P. praerutilum*, and thus is not helpful in diagnosing these taxa.

6. **Molars proportionately narrower with respect to their length, compared to *P. australe*:** Sinclair (1909) also proposed this as a diagnostic character for *P. praerutilum*. Our data clearly demonstrate this not to be the case (see table 2.6 and above discussion).
7. **The length/width ratio of the palate is intermediate between *P. australe* and *P. attennuatum*, in adult specimens:** We tentatively accept this as a useful distinction between *P. attenuatum* and *P. praerutilum* (see Emended Diagnosis, fig. 2.8, and table 2.7), and note that the relatively broad palate of *P. attenuatum* may be related to its highly curved dental series (especially P2-M3) (we measured palate width at the paraloph of M1, which is near the "apex" of this curvature in *P. attenuatum*). These conclusions, however, are based on just one specimen of *P. attenuatum* (MACN-A 4049) consisting of a fragmentary palate (our measurements, while necessarily inexact, are extremely close to their actual values, and accurately reflect the noticeably wide palate of this specimen). More complete specimens of *P. attenuatum* will help clarify the diagnostic utility of this character. Our data indicate that that the length/width ratio of the palate is generally not helpful in distinguishing *P. australe* and *P. praerutilum* (table 2.7).
8. **Short rostrum:** Tauber (1996) suggests this character is intermediate between *P. australe* ("long rostrum") and *P. attenuatum* ("very short rostrum"). We considered this character only qualitatively, and suspect that while it may not distinguish *P. australe* and *P. praerutilum*, it may distinguish *P. praerutilum* and *P. attenuatum*. More specimens of *P. attenuatum* need to be examined, and a standard by which to compare rostrum length quantitatively needs to be developed, before a definitive conclusion may be reached on this point.

9. **Very horizontal mandibular symphysis:** Our qualitative and cursory observations of this character suggest that it is similarly variable in *P. australe*, *P. praerutilum*, and *P. attenuatum*. We do not regard it as a useful diagnostic character.
10. **Implantation of the incisors more vertical compared to those of *P. australe***: Our qualitative and cursory observations suggest that this character is similarly variable in *P. australe*, *P. praerutilum*, and thus that it is not diagnostically useful.

We tentatively recognize three characters as reliably distinguishing *P. praerutilum* from *P. attenuatum*: *P. praerutilum* has a larger upper size limit (with overlap between *P. attenuatum* and smaller specimens of *P. praerutilum*); the upper dental series (especially P2-4) of *P. praerutilum* is less curved; and its palate is narrower (i.e., the palate length/width ratio is higher). These conclusions require the following caveats: 1) we examined few specimens of *P. attenuatum*, and even fewer that were complete enough to ascertain the latter two proposed diagnostic characters; 2) the type specimen of *Patriarchus* (=*Protypotherium*) *diastematus* (MACN-A 4044) possesses a mixture of these supposedly diagnostic characters (see discussion of *Protypotherium attenuatum* and *Patriarchus diastematus* in appendix 2.4); 3) based on this diagnosis, *Patriarchus rectus*, which both Sinclair (1909) and Tauber (1996) synonymized with *Protypotherium attenuatum*, should instead be synonymized with *P. praerutilum* (see appendix 2.4); and 4) based on this diagnosis, several well-preserved specimens currently labeled as *P. attenuatum* instead likely represent *P. praerutilum* (e.g., YPM-PU 15665 and AMNH 9187). We recognize that these ambiguities may reflect an underlying issue: *P. paerutilum* and *P. attenuatum* may simply represent end-members of intraspecific variation within a single taxon. If this proves to be

the case, *P. praerutilum* would have priority – both taxa were described by Ameghino (1887b) in the same paper, but *P. praerutilum* was considered first.

Interatheriinae indeterminate

MATERIAL: SGOPV 3794, a fragmentary mandibular symphysis bearing three teeth (?incisors) of uncertain position.

DISTRIBUTION AND AGE: This specimen was collected at locality C-02-7, within the Trapa Trapa East collecting area, approximately 10 km south of Laguna del Laja (LdL) (figs. 2.1 and 2.2). This is one of only three specimens collected from a volcaniclastic cobble conglomerate of the Trapa Trapa Formation (TTF; unit $Ttt_1$; Herriot, 2006). SGOPV 3794 is the first fossil formally described from the TTF. The age of SGOPV 3794 cannot be precisely determined – radioisotopic ages have only been obtained from overlying and underlying units. A basaltic andesite flow in the overlying $Ttt_2$ (TTF) was dated to 8.9 ± 0.10 Ma (sample CH-20), and an ignimbrite near the base of the underlying unit (Tcm2, Cura-Mallín Formation) was dated to ~14.50 ± 0.50 Ma (Herriot, 2006; Flynn *et al*. 2008) (fig. 2.2). In the studies area, unit $Ttt_1$ is bounded by fault splays that separate it from units $Ttt_2$ and $Tcm_2$, such that the true stratigraphic displacement of SGOPV 3794 from these dated horizons is unknown.

DESCRIPTION: These three teeth are likely either right i1 and left i2-3, or left i1-3. For the sake of convenience, we refer to these teeth as left i1-3. All teeth, and portion of mandibular symphysis in which they are embedded, are extremely fragmentary, making any identification difficult. The size of the symphysis and incisors, the procumbence of the

incisors, the general morphology of the teeth (columnar, but becoming mesiodistally longer and labiolingually flatter towards the top of the crown), and the record of interatheriids in the LdL region, all suggest that this specimen likely pertains to Interatheriinae. The procumbent incisors (character 20, state 1) also suggest that this specimen may be referable to either the "*Protypotherium* and allies" clade or the "*Interatherium* and allies clade" (see fig. 2.9). The fragmentary condition of this specimen precludes any more specific designation. The first incisor appears generally columnar, but the crown is broken occlusally and labially. The second incisor, which is somewhat smaller than i1 (although this size difference could be a result of breakage), is also generally columnar, but apparently becomes mesiodistally longer towards the top of the crown, which is broken occlusally and labially. The third incisor is columnar at the base, but becomes distinctly longer and flatter towards the top of the crown (though this could be a result of distortion); it is broken occlusally, mesially, and labially. The lingual margin of i3 also bears a vertical groove, but it is difficult to determine whether this is a natural feature or a result of breakage. The approximate measurements of these teeth are listed below:

- i1: mesiodistal length, 2.0 mm; labiolingual width, 1.5 mm.
- i2: mesiodistal length, 1.6 mm; labiolingual width, 1.2 mm.
- i3: mesdiodistal length, 2.0 mm; labioingual width, 1.7 mm.

## Phylogenetic Considerations

The description of several new taxa from the Andes of Chile provides an opportunity to reexamine and expand upon several previous studies of interathere relationships (Cifelli, 1993; Hitz *et al*., 2000, 2006, 2008; Reguero *et al*., 2003; Reguero and Prevosti, 2010). Here we emphasize the phylogeny of the Interatheriinae. Membership of the Interatheriinae and Notopithecinae has changed drastically since these groups were originally proposed. Indeed, for Ameghino, Interatheriinae (1887b) was intended to encompass what is today considered the Interatheriidae, while Notopithecinae (1897) included *Notopithecus adapinus* along with 'other' primates. Riggs and Patterson (1935) recognized the affiliation of *Notopithecus* and interatheriids, observing that in both, the maxilla excludes the jugal from the orbit. Simpson (1945, 1967) formalized this observation by dividing interatheres into the "early" (Mustersan and earlier), low-crowned Notopithecinae, and the "late" (Deseadan and later), hypsodont Interatheriinae, a taxonomic grouping that still influences modern interpretations (see McKenna and Bell, 1997; Reguero *et al*., 2003; Reguero and Prevosti, 2010). Recent studies have provided strong support for the monophyly of Interatheriidae (Billet, 2010; Cifelli, 1993; Hitz *et al*., 2000, 2006; Reguero and Prevosti, 2010), but it has become increasingly apparent that "Notopithecinae" is paraphyletic (Hitz *et al*., 2000, 2006; Reguero and Prevosti, 2010). On the other hand, even the first cladistic treatment of interatheres suggested that the Interatheriinae are monophyletic (Cifelli, 1993), and this has been subsequently confirmed by numerous subsequent cladistic analyses (Hitz *et al*., 2000, 2006, 2008; Reguero *et al*., 2003; Billet, 2010; Reguero and Prevosti, 2010). Despite widespread recognition of interatheriine monophyly, the precise definition and taxonomic membership

of Interatheriinae remains in flux, as do hypotheses of the phylogenetic relationships among interatheriines.

Simpson (1945) assigned all Deseadan and post-Deseadan interatheres to the Interatheriinae. These include *Cochilius*, *Archaeophylus*, *Plagiarthus*, *Protypotherium*, *Interatherium*, *Medistylus*[1], *Paracochilius*, *Epipatriarchus*, and *Caenophilus*. Since then, Reguero *et al*. (2007) recovered more complete specimens of *Medistylus* and re-assigned this taxon to the Hegetotheriidae. Further, *Paracochilius*, *Epipatriarchus*, and *Caenophilus*, based on poorly known and/or fragmentary materials, have been excluded from recent treatments of interatheriine relationships (Hitz *et al*. 2000; 2006; 2008; Reguero 1999; Reguero and Prevosti 2010; Reguero *et al*., 2003). Similarly, these genera are excluded from the present analysis, a decision we make without implications concerning the taxonomic status of these taxa. With regard to the Interatheriinae, Simpson (1967, p 74) noted a "profound phylogenetic gap" between interatheriines and their early diverging counterparts, the "notopithecines." As recently described taxa have helped close this gap, various definitions and diagnoses for Interatheriinae have been proposed (Hitz *et al*., 2000, 2006, 2008; Reguero *et al*., 2003; Reguero and Prevosti, 2010).

Before discussing the most recent cladistic and taxonomic treatments of the Interatheriinae, we should emphasize the continuing pertinence of Cifelli's (1993) conclusions in his pioneering cladistic analysis of notoungulates. Although Cifelli's (1993) results supported interatheriine monophyly, he noted that insufficient data and an apparently high degree of homoplasy prevented any strong conclusions concerning relationship *within*

[1] This taxon was originally given the preoccupied name *Phanophilus dorsatus* by Ameghino (1903). Stirton (1952) renamed the genus *Medistylus*.

the clade. Indeed, his analysis resulted in a single polytomy from which stemmed all interatheriine genera (including *Plagiarthus*, *Cochilius*, *Miocochilius*, *Interatherium*, *Archeophylus*, *Progaleopithecus*, *Epipatriarchus*, and *Protypotherium*) (Cifelli, 1993). Cifelli (1993) did, however, informally recognize two distinct groups within the Interatheriinae – one including *Protypotherium* and its allies, and the other *Interatherium* and its allies (a suggestion also enunciated earlier; Cifelli, 1985; MacFadden *et al*., 1986; Marshall *et al*., 1986). The validity of these two apparent subgroups, along with uncertainty about interatheriine relationships and high degrees of homoplasy, will be further discussed below.

Hitz *et al*. (2000) offered the first phylogenetic definition of Interatheriinae, applying this name to the clade stemming from the most recent common ancestor of *Interatherium* and *Santiagorothia*, the latter of which was described in that study. The authors used *Santiagorothia* as a specifier in their definition because it was the earliest interathere known from reasonably complete material that exhibited large size and hypsodonty – two characters traditionally associated with interatheriines (Simpson, 1967; Cifelli 1985). *Eopachyrucos* and *Proargyrohyrax*, although not included in Hitz *et al*.'s (2000) phylogenetic analysis, were considered interatheriines because they appeared to possess the clade's diagnostic features. Also, *Federicoanaya sallensis* and *Brucemacfaddenia boliviensis*, then unnamed taxa based on material from Bolivia (more thoroughly addressed in Hitz *et al*., 2006), were regarded as members of Interatheriinae.

In a subsequent cladistic analysis incorporating *Eopachyrucos* and *Proargyrohyrax*, Hitz *et al*. (2006) identified *Eopachyrucos* as the closest outgroup to Interatheriinae (*sensu* Hitz *et al*., 2000), making hypsodonty no longer diagnostic of interatherrines (given their exclusion of the hypsodont *Eopachyrucos*). Anticipating that these new findings might be

used to overturn the definition that Hitz *et al*. (2000) applied to Interatheriinae, Hitz *et al*. (2006) reasoned that this phylogenetic definition remained a stronger option than an apomorphy-based phylogenetic definition that attempts to preserve the historical linkage between hypsodonty and the name Interatheriinae. Hitz *et al*. (2006) emphasized that 1) hypsodonty is by nature a gradational character, and 2) the "profound phylogenetic gap" Simpson observed between "notopithecines" and "interatheriines" had been substantially narrowed by recently described taxa. These intermediate taxa display a sequential acquisition, over a long time span, of characters once thought to be clearly diagnostic of Deseadan and younger interatheriids. We further note that it is risky to use the appearance of an apomorphy to phylogentically define a taxonomic name when that apomorphy (hypsodonty) has clearly evolved convergently numerous times within notoungulates.

Although we support a node-based definition of Interatheriinae, we note that an alternative phylogenetic definition has been applied by Reguero *et al*. (2003) and Reguero and Prevosti (2010). These authors define Interatheriinae as the clade stemming from the most recent common ancestor of *Eopachyrucos* and *Interatherium*. The advantage of specifying *Eopachyrucos* in this definition is that 1) hypsodonty remains diagnostic of Interatheriinae, 2) the node that encompasses *Eopachyrucos* and all later diverging interatheriines is among the best supported nodes in analyses by Hitz *et al*. (2006) and Reguero *et al*. (2003), as well as in the present study; and 3) the node from which *Santiagorothia* arises and which excludes *Eopachyrucos* (and in some cases *Proargyrohyrax*) is poorly supported in all three studies (Hitz *et al*., 2006; Reguero *et al*., 2003; present study). Conversely, there are also advantages of using *Santiagorothia* to define the Interatheriinae: 1) it has priority as the first phylogenetic definition of Interatheriinae proposed, and 2) *Santiagorothia* is known from more complete material than is

*Eopachyrucos*. We acknowledge that both options have strengths and weaknesses, but we wish to emphasize the importance of using well-supported nodes to define widely used names. As such, we adopt the definition proposed by Reguero *et al*. (2003), and regard the Interatheriinae as the clade stemming from the last common ancestor of *Eopachyrucos* and *Interatherium*. A consequence of this decision, we acknowledge, is that phylogenetic definitions of some names may change as nodal support within phylogenies shift.

The cladistic analyses of Hitz *et al*. (2000, 2006) were among the most thorough treatments of interathere relationships of the time, but numerous nodes remained highly polytomous. In the more recent and comprehensive of these analyses (Hitz *et al*., 2006), for example, the 11 interatheriines were resolved into five nodes, three of them polytomies. Incorporating fewer interathere taxa, the studies of Reguero *et al*. (2003) and Reguero and Prevosti (2010) produced more highly resolved phylogenies than those of Hitz *et al*. (2000; 2006). Here we discuss the results of the former study (Reguero *et al*. 2003), which focused exclusively on interathere relationships and included more interatheriine taxa than the later effort (Reguero and Prevosti, 2010). The analyses of Reguero *et al*. (2003) and Hitz *et al*. (2000, 2006) yielded significantly different hypotheses of relationship *within* the Interatheriinae. Notable among these are the phylogenetic positions of *Plagiarthus* and *Progaleopithecus*. While Reguero *et al*. (2003) placed these two taxa at relatively basal positions within the clade, Hitz *et al* (2000, 2006) identified a polytomy joining *Protypotherium*, *Miocochilius*, and *Progaleopithecus*, and placed *Plagiarthus* as the proximal outgroup to *Cochilius* plus *Interatherium*.

The current study was undertaken with the expectation that the new taxa from LdL would help to clarify interatheriine relationships, adding to an existing body of work that has significantly advanced our understanding of the Interatheriinae.

Several features of our phylogeny merit discussion. First, this analysis provides a clear step toward resolving some of the polytomies that bedeviled previous studies (Cifelli, 1993; Hitz *et al*., 2000, 2006, 2008), while simultaneously incorporating more interatheriine taxa than previous efforts (Cifelli, 1993; Hitz *et al*., 2000, 2006, 2008; Reguero *et al*., 2003; Reguero and Prevosti 2010). For example, the phylogeny produced by Hitz *et al*. (2000, 2006, 2008) included three polytomies in a tree of 12 interatheriines (*sensu* Reguero *et al*. 2003), while the analysis of Reguero *et al*. (2003) included 10 interatheriines, with two tritomies. The phylogeny presented here, on the other hand, includes 15 interatheriine taxa and a single polytomy.

Needless to say, our results do not warrant complete confidence in every proposed relationship. Indeed, as in previous studies (Cifelli, 1993; Reguero *et al*., 2003), we report a high degree of homoplasy. The prevalence of homoplasy is evident in: 1) character mapping (fig. 2.9; homoplastic characters are indicated by open squares and circles); 2) the low CI (0.59) and RI (0.67) of the consensus tree; and 3) many nodes with low node support (fig. 2.9). In particular, we note that the homoplasious characters shared by *Miocochilius* and members of the clade that include *Archeophylus*, *Interatherium*, and *Cochilius* (characters 23, 30, 31) suggest that future fossil discoveries and phylogenetic analyses may refine these relationships. Indeed, the proposed relationship between *Progaleopithecus* and *Miocochilus* represents one of the most poorly supported nodes of our tree (fig. 2.9). Moreover, while the significant gap in geographic and temporal occurrence of these two taxa (*Progaleopitecus* is known from the Deseadan of Patagonia; *Miocochilius* from the Laventan of Colombia) does not completely preclude their close relationship, this gap, combined with aforementioned homoplasies, compels caution concerning the phylogenetic position of these taxa.

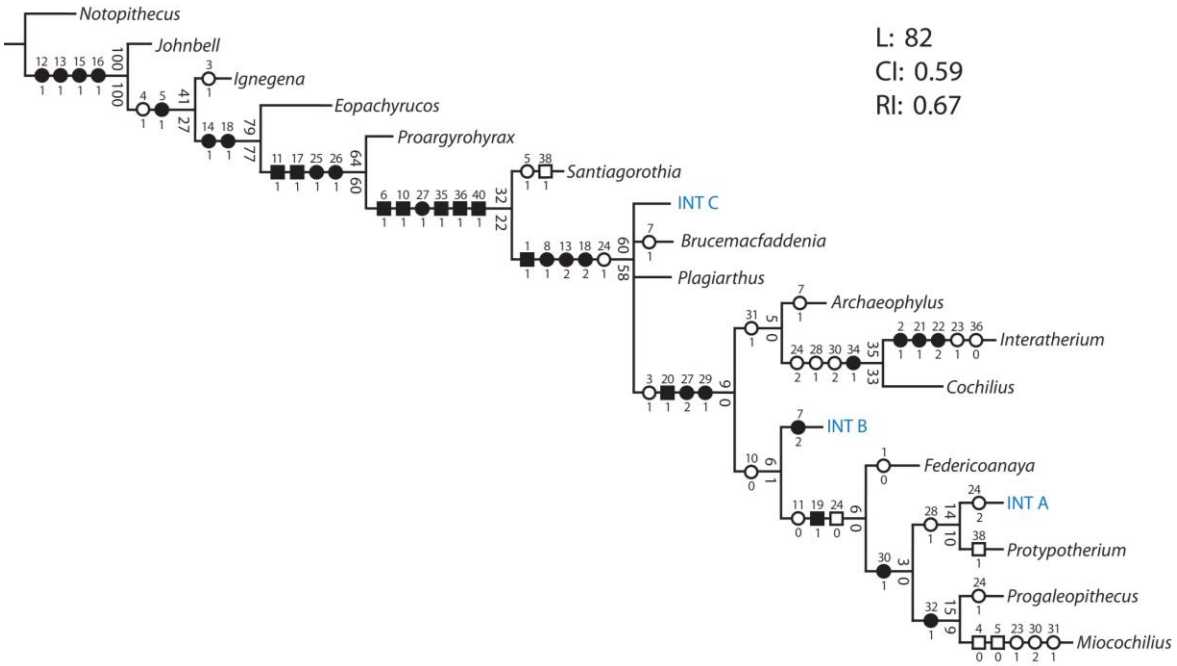


FIGURE 2.9. Strict consensus tree of Interatheriinae (and outgroups: *Notopithecus*, *Johnbell*, and *Ignegenia*). Synapomorphies indicated by circles or squares, with character numbers above and character states below (see appendix 1 for character descriptions). Squares indicate an equivocal condition in which the outgroup to the clade is missing data for that character. Open squares and circles are homoplasies. At the base of each node are the confidence scores from symmetric resampling; above the node are absolute frequencies and below the node are relative frequencies. Abbreviations: L, length; CI, consistency index; RI, retention index.

The uncertainly in these phylogenetic results is also compounded by missing data, the influence of which can be seen by the number of characters representing an equivocal condition, in which the character states of the outgroup(s) to a clade could not be determined (these equivocal characters are indicated by squares in fig. 2.9).

The above caveats aside, we remain confident that this phylogeny offers at least a modest contribution towards clarifying interatheriine relationships. These results allow us to address previous, conflicting interpretations of interatheriine interrelationships – specifically, some of the disagreements between the results of Hitz *et al*., (2000, 2006, 2008) and Reguero *et al*. (2003) – as well as to suggest more highly resolved hypotheses of interatheriine relationships, providing a phylogenetic framework to be tested by future research.

Regarding the phylogenetic definition of Interatheriinae, we reiterate that our results provide further grounds to adopt the usage of Reguero *et al*. (2003) and Reguero and Prevosti (2010), who defined Interatheriinae as the clade stemming from the most recent common ancestor of *Eopachyrucos* and *Interatherium*. Alternatively, Hitz *et al*. (2000, 2006, 2008) proposed a phrasing that excluded *Eopachyrucos* from membership in the clade thusly named (Hitz *et al*., 2006, 2008). Our analysis indicates that the node giving rise to *Eopachyrucos* and all later diverging interathere is among the best supported of the entire tree, whereas the node from which *Santiagorothia* and later diverging interatheres arise (to the exclusion of *Eopachyrucos* and *Proargyrohyrax*) is weakly supported (fig. 2.9). A similar pattern of nodal support was observed by Hitz *et al*. (2006). Furthermore, in all analyses in which the placement of *Eopachyrucos*, *Proargyrhoyrax*, and *Santiagorothia* is resolved, *Eopachyrucos* consistently falls as the earliest diverging of the three (Hitz *et al*., 2006, 2008; Reguero *et al*., 2003; Reguero and Prevosti, 2010), increasing confidence in the stability of this topology. While the definitions of Interatheriinae of Hitz *et al*. (2000) and Reguero *et al*. (2003) both have merits (see above), we are ultimately persuaded that, whenever possible, node-based definitions should be applied to well-supported nodes. It is our expectation that the definition of Interatheriinae proposed by Reguero *et al*. (2003) will prove maximally stable, and therefore useful. Interatheriinae (*sensu* Reguero *et al*., 2003) is diagnosed by upper molars with a reltively flat ectoloph lacking a pronounced metacone bulge (character 14, state 1) and hypsodont posterior premolars and molars (character 18, state 1). In addition, the optimization of characters 6, 10, 11, 17, 33, 35, 36, 40 are uncertain (fig. 2.9) – a result of *Eopachyrucos* and *Proargyrohyrax* being known from only partial dentitions – and we suspect that, with the recovery of more complete specimens, many of these characters may eventually be used to diagnose Interatheriinae, as well.

In terms of relationships *within* the Interatheriinae, the most significant differences between the analyses of Reguero *et al*. (2003) and Hitz *et al*. (2000, 2006) involve the placement of *Plagiarthus* and *Progaleopithecus*. Results of the current analysis concord with the arrangement of Reguero *et al*. (2003) in that *Plagiarthus* occupies a fairly basal position within Interatheriinae. This contrasts with the results of Hitz *et al*. (2000, 2006), where *Plagiarthus* is placed outside a pairing of *Cochilius* and *Interatherium*. The more basal position of *Plagiarthus* is supported by the retention of two primitive characters that merit note: it possesses a metacristid on the trigonid of p4-m3 (character 27, state 1) and a lingual sulcus on the trigonid of m1-3 (character 29, state 0). With regard to *Progaleopithecus*, our analysis supports a close relationship between *Miocochilius* and *Progaleopithecus*, consistent with the previous findings of Hitz *et al*. (2000, 2006). However, this arrangement is weakly supported (fig. 2.9); it is hoped that future research will provide a more securely established phylogenetic position of *Progaleopithecus*.

Our results also resolve phylogenetic hypotheses within two, long informally recognized groups of interatheriines: "*Protypotherium* and allies" and "*Interatherium* and allies" (Cifelli, 1985; MacFadden *et al*., 1986; Marshall *et al*., 1986; Hitz *et al*., 2000, 2006; Reguero *et al*., 2003). In a phylogenetic context, "*Protypotherium* and allies" would correspond to the clade that includes INT B, *Federicoanaya*, INT A, *Progaleopithecus*, *Miocochilius*, and *Protypotherium*, while "*Interatherium* and allies" would include *Archeophylus*, *Cochilius*, and *Interatherium*. Not only are these groups identified as monophyletic individually, but also as a pair. Together, these taxa constitute a clade of late-diverging interatheriines diagnosed by the relatively slender lower canine (character 3, state 1), the absence of a metacristid on p4-m3 (character 27, state 2), and the absence of a lingual sulcus on the trigonid of the lower molars (character 29, state 1).

These two interatheriine groups have previously been identified primarily on the basis of molarization of the upper molars. Indeed, our results suggest that the morphology of interathere upper premolars have a complex and phylogenetically informative evolutionary history. Basal interatheres (represented herein by *Johnbell*, *Ignigena*, and *Notopithecus*) are characterized by pre-molariform upper premolars – somewhat triangular in shape and lacking the highly developed protoloph of the molars (characters 9-11, state 0). Early in the evolution of interatheriines (the precise phylogentic position is difficult to determine due to the incompletely known dentitions of *Proargyrohyrax* and *Eopachyrucos*) upper premolars developed larger protolophs and a more rectangular occlusal outline, thus more closely resembling the molars. Later diverging interatheriines, specifically the clade that includes both "*Interatherium* and allies" and "*Protypotherium* and allies" (see above), can broadly be divided on the basis of whether or not this premolar shape was maintained. The "*Interatherium* and allies" clade retained molariform upper premolars, whereas the "*Protypotherium* and allies" clade appears to have gradually reverted to a seemingly more primitive condition, developing "non-molariform" upper premolars more similar to those of the earliest interatheres (fig. 2.10). In particular, our results place INT B in a transitional position, displaying a premolariform P3 (character 10, state 0) but a molariform P4 (character 11, state 1), while *Federicoanaya*, *Protypotherium*, and *Miocochilius* have premolariform P2-4 (characters 9-11, state 0; the upper premolars of INT A and *Progaleopithecus* are unknown) (fig. 2.10). The presence of a molarized P2 in *Brucemacfaddenia*, *Archeophylus*, and *Interatherium* (character 9, state 1), cannot be clearly interpreted in this phylogenetic context (i.e., the optimization of character 9 is ambiguous, and was not included in fig. 2.9).

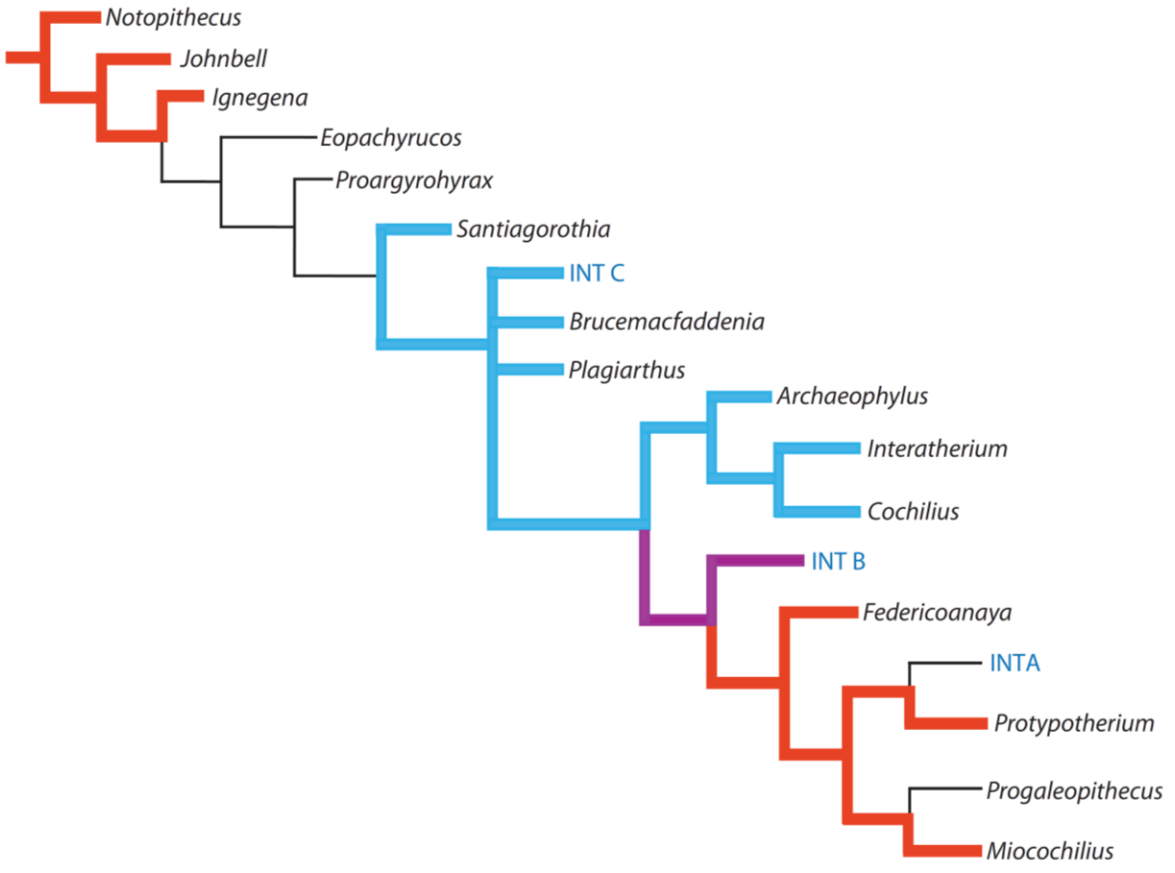


FIGURE 2.10. Phylogeny of Interatheriinae (and outgroups: *Notopithecus*, *Johnbell*, and *Ignegenia*), highlighting the evolution of premolar morphology. Red bars indicate "premolarifrom" P3-4 (characters 10 and 11, state 0; see appendix 1 for more detailed character descriptions). Blue bars indicate "molarized" P3-4 (characters 10 and 11, state 1). Purple bars indicate "premolarized" P3 and "molarized" P4. Black lines indicate missing data.

Having considered the phylogenetic position of INT B, we shift attention to the other new taxa described here. The relationships of INT C are poorly resolved, as this taxon falls within a polytomy including *Plagiarthus* and *Brucemacfaddenia*. (The affinities between INT C and *Plagiarthus* were discussed above; see Systematic Paleontology). INT A and *Protypotherium* are united by a single synapomorphy – the relatively large size of the lower molar talonids (character 28, state 1). The clade including INT A, *Protypotherium*, *Progaleopithecus*, and *Miocochilius* is diagnosed ancestrally by triangular m2-3 trigonids (character 30, state 1). The m2-3 trigonids of *Miocochilius*, however, are semicircular (state 2). In the context of the phylogeny advocated here, the relatively large p2-4 talonids of INT A and *Interatherium*/*Cochilius* (character 24, state 2) are interpreted as convergently acquired.

The three taxa described herein belong to a diverse clade of hypselodont interatheriines (figs. 2.9, 2.11). Interatheres reached their highest diversity during the Deseadan SALMA (Late Oligocene), a radiation corresponding with the development of hypsodonty and hypselodonty (Marshall and Cifelli, 1990; Reguero, 1999; Hitz *et al*. 2000, 2008; Reguero *et al*., 2003). The importance of hypselodontly in the evolution of interatheriines is highlighted in fig. 2.11. Hypselodont interatheriines are first known from the Deseadan, suggesting that hypselodonty arose in this clade sometime between the Tinguiririan and Deseadan (mid Oligocene?). High interatheriine diversity during the Deseadan (at least six genera are known from this SALMA) is very likely tied to the acquisition of hypselodonty, but our analysis further indicates that even later diverging groups, such as the aforementioned "*Interatherium* and allies" and "*Protypotherium* and allies" clades, appear to have their roots in a Deseadan radiation, as well.

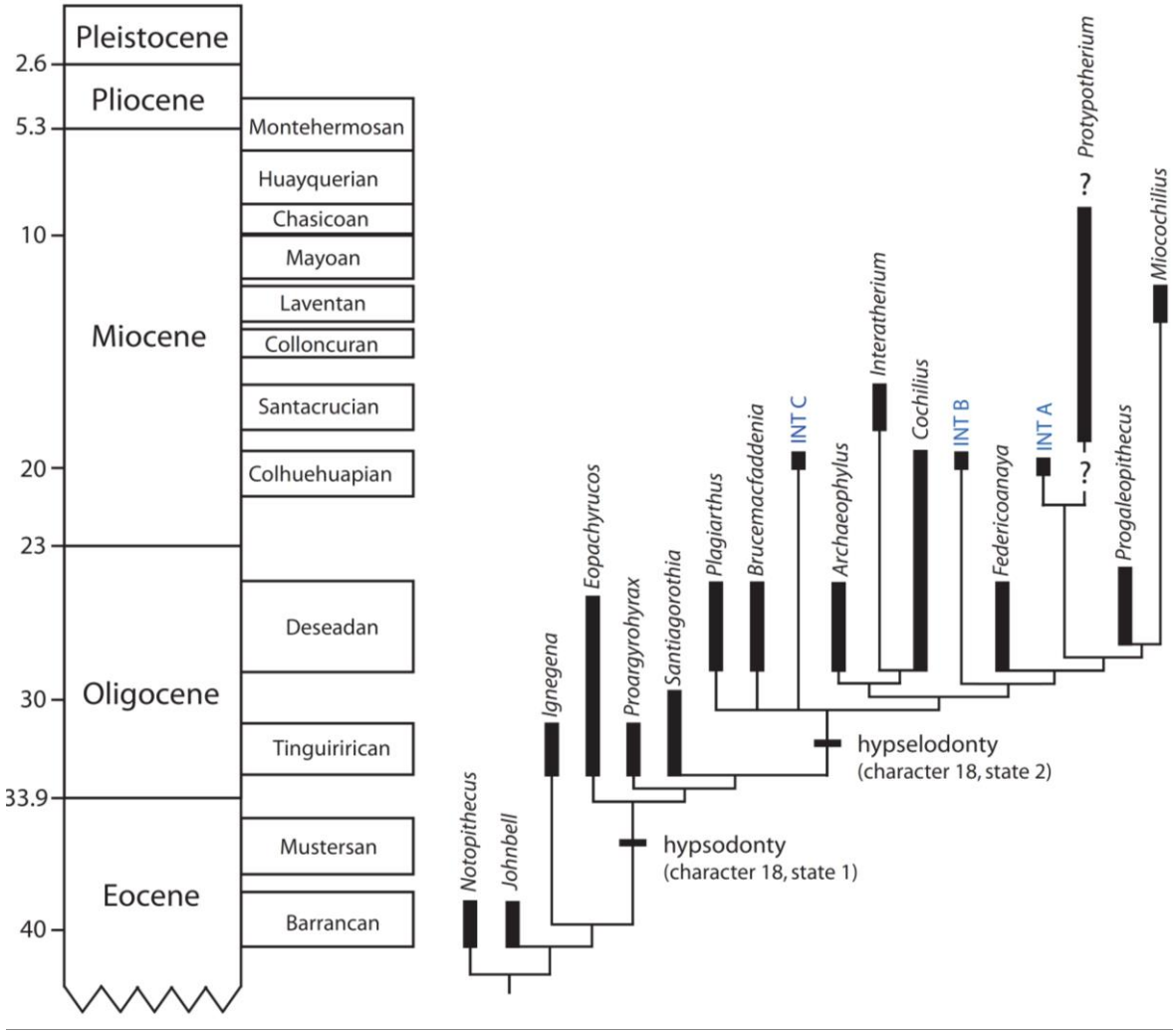


FIGURE 2.11. Phylogeny of Interatheriinae (and outgroups: *Notopithecus*, *Johnbell*, and *Ignegenia*), with the temporal range of each taxon indicated by black bars.

# Summary and Conclusions

In this study we describe three new interatheriines from the Andes of central Chile, ranging in age from ~20-19 Ma. We build upon previous analyses of interatheriine phylogenetic relationships, in part by incorporating these new taxa. Three specimens from coeval and younger stratigraphic horizons at Laguna del Laja (LdL) are referred to *Protypotherium praerutilum*, prompting a preliminary revision of *Protypotherium*. Our findings our summarized below:

**New interatheriines from the Andes of central Chile:** Of the three new taxa are described here, INT A is recognized on the basis of two specimens recovered from exposures of the Cura-Mallín Formation (CMF) along Estero Correntoso, immediately south of LdL. The stratigraphic position of these specimens suggests an age of ~19 Ma. Known primarily from lower dentitions, INT A displays a suite of characters that resemble *Protypotherium* in some respects and *Interatherium*/*Cochilius* in others. Parsimony analysis indicates that INT A and *Protypotherium* are mutual nearest relatives, implying that the similarities between INT A and *Interatherium*/*Cochilius* are the result of convergence. From stratigraphically lower exposures of the CMF along Estero Correntoso (~19.5 Ma), INT B is recognized on the basis of a nearly complete upper dentition. INT B is distinguished by several unique characters, including the apparently transitional combination of molariform P4 and premolariform P3. Consistent with this observation, INT B falls phylogenetically between earlier-diverging interatheriines with molariform P3-4 (e.g. *Plagiarthus*, *Brucemacfaddenia*, INT C, and *Santiagorothia*), and some later-diverging interatheriines with pre-molariform P3-4 (e.g. *Federicoanaya*, *Protypotherium*, and *Miocochilius*). INT C, the third new taxon, is known from two upper dentitions: one was recovered from exposures

of the CMF ~6 km north of LdL (the age and precise stratigraphic position of this specimen remain uncertain), and the other derives from the Abanico Formation along the southern slope of the Río Las Leñas valley (~300 km north-northeast of LdL), dated to ~20 Ma. Along with the other interatheriines described in this study, INT C is characterized by a hypselodont dentition; in this respect it is more derived than pre-Deseadan interatheriines. Although uniquely diagnosed by several features, including notably robust P2-M1, INT C is in many ways similar to *Plagiarthus*. Indeed, our cladistic analysis places INT C in a polytomy with *Plagiarthus* and *Brucemacfaddenia*.

**Preliminary revision of *Protypotherium*:** Four specimens recovered from LdL, ranging in age from ~19.5-17.7 Ma, are assigned to *Protypotherium praerutilum*, prompting a long-overdue taxonomic appraisal of the species and genus. Despite the welcome revision of Tauber (1996), our examination of dozens of *Protypotherium* specimens at numerous institutions has highlighted several persisting taxonomic problems. In summary: 1) Compared to other hypselodont interatheriines, *Protypotherium* is most readily diagnosed by "premolariform" upper premolars; a relatively large m1 talonid, m2-3 talonids that are sub-traingular with narrow anterior margins; a salient lingual sulcus on the m3 talonid (but no strong labial sulcus); i1-2 that are bicolumnar in early wear stages and become columnar with wear; and p2-4 talonids that are significantly smaller than their respective trigonids. 2) According to strict priority, *P. antiquum* Ameghino 1885 is the type species for the genus. However, *P. antiquum* is known only from one partial mandible with little diagnostic information – apart from a salient labial sulcus on the m3 talonid, which is absent among the best known species of *Protypotherium* (*P. australe*, *P. praerutilum*, and *P. attenuatum*). Accordingly, we regard *P. australe* as the genotype, even though it was initially described as *Toxodontophanus australis* (*nomen nudum* in Moreno, 1882; brief description in Ameghino,

1887a), and relegate ZMUC ZMK 21/1877 (the type of "*Protypotherium antiquum*") to Interatheriinae *incertae sedis*. 3) Most type specimens of species of *Protypotherium* are uncertainly identified; nonetheless, we have attempted to identify as much type material as possible (see table 2.4, appendix 2.4). 4) We concur with many synonymies proposed by Sinclair (1909) and Tauber (1996), but offer several emendations. In particular, *Protypotherium convexidens* is considered a *nomen nudum*; *Protypotherium compressidens* may be a valid taxon; *Patriarchus rectus* should be synonymized with *Protypotherium praerutilum* instead *of P. attenuatum*; *P. martini* should be synonymized with *P. australe*; and MACN 11742 (the holotype and only specimen of "*P. minor*") and MACN-A 4052 (the holotype and only specimen of "*P. diversidens*") should be considered Interatheriinae *incertae sedis*.

*P. australe, P. praerutilum,* and *P. attenuatum* are the best established species of *Protypotherium* (and we further recognize the validity of *P. compressidens*), but the characters previously used to diagnose these taxa are often not reliable. We assign three LdL specimens to *P. praerutilum,* resulting in an emended diagnosis of this species. Compared to *P. australe*, *P. praerutilum* is smaller (especially notable in palate length), and generally possesses I1 that is subequal in size to I2/3. Compared to *P. compressidens*, the upper molars of *P. praerutilum* are wider labiolingually (relative to upper molar length). We provisionally recognize *P. praerutilum* and *P. attenuatum* as valid, and propose the following characters as distinguishing: compared to *P. attenuatum*, *P. praerutilum* has a larger upper size limit (with overlap between *P. attenuatum* and smaller specimens of *P. praerutilum*); a straighter upper tooth row (especially P2-4); and a narrower palate.

The taxonomic remarks offered above are intended as a foundation for further revision of this well-known (and prolifically represented) taxon, and we encourage

reevaluation of *Protypotherium* material in museum with these suggestions in mind. This effort will surely provide a clearer understanding of the temporal range and geographic occurrences of *Protypotherium* and its constituent species.

**Phylogeny of Interatheriinae:** Using an updated character matrix and incorporating the taxa described herein, the phylogenetic work carried out in this study advances our understanding of interatheriine evolution. We adopt the phylogenetic definition of Interatheriinae (Reguero *et al*., 2003) as the clade stemming from the most recent common ancestor of *Eopachyrucos* and *Interatherium*. Our phylogeny is marked by a high degree of homoplasy, one unresolved polytomy, and low confidence for several nodes, underscoring the provisional nature of some of the relationships proposed herein. Nonetheless, these results provide a greater resolution than available previously, allowing us to advance new hypotheses concerning interatheriine evolution. In particular, our analysis better resolves two sub-clades that have long been informally recognized – the so-called "*Protypotherium* and allies" and "*Interatherium* and allies" (Cifelli, 1985; MacFadden *et al*., 1986; Marshall *et al*., 1986; Hitz *et al*., 2000, 2006; Reguero *et al*., 2003). The earliest interatheres, such as *Notopithecus, Ignigena,* and *Johnbell*, possessed "premolariform" premolars that were sub-triangular in occlusal outline, bearing relatively small protolophs. Later-diverging taxa (e.g., *Santiagorothia, Plagiarthus,* and *Brucemacfaddenia*) developed more molariform premolars (in particular P3-4), with larger protolophs giving these teeth a more rectangular shape. The "*Interatherium* and allies" clade maintained this derived condition, while the "*Protypotherium* and allies" clade underwent a reversal, with premolars returning to a "premolariform" arrangement. INT B, marked by a premolariform P3 and a molariform P4, is a transitional taxon, bridging early interatheriines (with molariform P3-4) and the "*Protypotherium* and allies" clade (with premolariform P3-4). Interatheriines, first known

from the Tinguiririan SALMA, attained hypselodonty by the Deasadan, coinciding with a marked diversification of the clade (fig. 2.11). The roots of the "*Protypotherium* and allies" and "*Interatherium* and allies" clades lie within this Deseadan radiation.

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Appendix 2.1: Characters and character states used in the phylogenetic analysis.

Comparisons and modifications to recent phylogenetic analyses of interatheriid relationships (Reguero *et al*., 2003; Hitz *et al*., 2006) are noted for each character. There were several characters coded by Hitz *et al*. (2006) that were not included in the present analysis because they were not informative for the taxa included herein; these include characters 2, 30, 31, 37, 41, 42 from Hitz *et al*. (2006). There were several additional characters coded in previous studies that were not included in the present analysis because they were unclear, difficult to objectively assess, and/or variable within several taxa; these include characters 9,13, 21, 26, and 43 from Hitz *et al*. (2006), and character 27 from Reguero *et al*., (2003). Characters 7 and 31 are new characters, and not simply rewritten or rescored based on previous studies. All characters treated as unordered.

1. **I1 size:** (0) subequal to or slightly larger than other anterior teeth; (1) greatly enlarged.

This is character 1 in Hitz *et al*., 2006, and similar to character 0 in Reguero *et al*., 2003. *Protypotherium* was scored as variable for this character, since *P. australe* has enlarged an enlarged I1, but *P. praerutilum* commonly has an I1 that is subequal in size to I2.

2. **I2-3 size**: (0) subequal; (1) reduced, with I3 smaller than I2.

This is character 4 in Hitz *et al*., 2006.

3. **C size:** (0) subequal in size to P1; (1) subequal in mesiodistal length, but notably narrower labiolingually than P1.

This is similar to character 3 in Hitz *et al*., 2006, which described the canine as either "large" or "reduced." Our character descriptions clarify this morphology, resulting in different scoring for almost all taxa.

4. **C exterior face**: (0) convex or vague anterior swelling; (1) distinct and persistent vertical anteroexternal ridge.

This is similar to character 5 in Hitz *et al*., 2006, which includes I2-3 in the character description. We limit this character to the canine, since in the incisors this feature was either variable within a taxon (e.g., *Santiagorothia* and *Protypotherium*) or difficult to assess objectively. Also, the character description was slightly modified to emphasize the persistence of this character with wear. *Ignigena* is the only taxon scored differently from the data matrix in Hitz *et al*., 2006, since the published figures of the type specimen (figs. 7 and 8 in Hitz *et al*., 2006) appear to confirm the presence of a distinct anteroexternal ridge on the upper canine (character state 1) of this taxon.

5. **P1 vertical anteroexternal ridge**: (0) ridge extremely vague or absent; (1) salient ridge present.

This is similar to character 6 in Hitz *et al*., 2006. The character state descriptions were slightly clarified. *Miocochilius* was scored differently than in Hitz *et al*., 2006, since no salient ridge on P1 was observed in the specimens examined. Also, we found that this character was variable within *Protypotherium* and *Interatherium*.

6. **P2-4 parastyle/paracone inflection**: (0) absent or broad; (1) distinct and narrow sulcus.

This is similar to character 7 in Hitz *et al*., 2006, and character 12 in Reguero *et al*., 2003. Character descriptions were rewritten for greater clarity, resulting in numerous scoring differences compared to these previous studies.

7. **Relative sizes of P2-4 parastyle/paracone inflection:** (0) subequal in size from P2-4 or a slight increase in size from P2-4; (1) P2 inflection clearly deepest; (2) P4 significantly deeper than P2/3.
8. **P3-4 fossettes and internal sulcus**: (0) anterior, posterior, and lingual fossettes moderately to strongly persistent, (1) lingual remains open as a sulcus, others disappear rapidly with wear.

This is character 8 in Hitz *et al*., 2006.

9. **P2 molarization and occlusal shape**: (0) premolariform: subtriangular and notably distinct from molars in lacking a well-developed protoloph and/or lack the lingual sulcus of the molars; (1) molariform: subquadrangular with a well-developed protoloph separated from the metaloph by a lingual sulcus.

Interatheriinae gen. *et* sp. *nov*. B (INT B) was scored as (0) for this character, even though the P2 is not preserved, because the P3 is premolariform. There is no instance in interatheres in which an anterior premolar is more molariform than the adjacent, posterior premolar. As such, we are confident assuming that the INT B possessed a premolariform P2.
10. **P3 molarization and occlusal shape**: (0) premolariform: subtriangular and notably distinct from molars in that they lack a well-developed protoloph and/or lack the lingual sulcus of the molars; (1) molariform: subquadrangular with a well-developed protoloph separated from the metaloph by a molar-like lingual sulcus.
11. **P4 molarization and occlusal shape**: (0) premolariform: subtriangular and notably distinct from molars in that they lack a well-developed protoloph and/or lack the lingual sulcus of the molars; (1) molariform: subquadrangular with a well-developed protoloph separated from the metaloph by a molar-like lingual sulcus.

Characters 9-11 are similar to character 13 in Reguero *et al*., 2003, and character 10 in Hitz *et al*., 2006. The character descriptions are made more explicit, focus more on shape rather than L/W ratios (as in Hitz *et al*., 2006), and P2-4 are considered separately. Accordinlgy, several taxa are scored differently than in previous studies.
12. **P2-4 cingulum**: (0) anterior cingulum low on crown; (1) anterior cingulum absent.

This is similar to character 11 in Hitz *et al*., 2006, but rewritten here to focus only on the anterior cingulum, since in all specimens examined the posterior cingulum (which is included as part of the character description in Hitz *et al*., 2006) is either absent or merges into the metaloph early with wear.
13. **M1-2 lingual sulcus and fossettes**: (0) anteroexternal, posteroexternal, and lingual fossettes present throughout most wear stages, lingual sulcus vague and/or reduced rapidly with wear; (1) moderately persistent lingual sulcus and fossette, other fossettes of varying longevity; (2) completely persistent lingual sulcus, fossettes absent or very rapidly disappear with wear.

This is character 13 in Hitz *et al*., 2006, and similar to character 7 in Reguero *et al*., 2003.
14. **M1-3 metacone ectoloph**: (0) distinct; (1) very low or flat.

This is character 15 in Hitz *et al*., 2006.
15. **M1-3 anterior cingulum**: (0) present and low and crown; (1) absent

This is character 16 in Hitz *et al*., 2006.
16. **M1-3 dimensions**: W (labiolingual) > L (mesiodistal), or equidimensional; (1) L (mesiodistal) > W (labiolingual).

This is character 17 in Hitz *et al*., 2006.
17. **M3 hypocone**: (0) absent or diminutive; (1) developed.

This is character 14 in Hitz *et al*., 2006.

18. **Crown height in posterior Ps and Ms**: (0) brachydont; (1) hypsodont; (2) hypseledont

This is character 18 in Hitz *et al*., 2006, and similar to character 3 in Reguero *et al*., 2003.

19. **Shape of i1-2**: (0) possessing one or two lingual grooves, and with mesiodistal length much greater than labiolingual width; (1) bicolumnar early in wear, and circular or ovoid in cross section in later wear stages.

This is similar to character 20 in Hitz *et al*., 2006, and character 18 in Reguero *et al*., 2003. The character description was rewritten for greater clarity. In Hitz *et al*., 2006, this character was scored as (?) for *Plagiarthus*, but based on the description in Reguero, 1999, and the dataset in Reguero *et al*., 2003, this taxon is scored as (0) herein. Hitz *et al*. (2006) only had access to specimens of *Plagiarthus clivus* (our observations in this study are also limited to specimens of *P. clivus*), whereas Reguero (1999) and Reguero *et al*. (2003) examined the anterior dentition of *P. proavunculus*. Also, note that Interatheriinae gen. *et* sp. *nov*. A and *Miocochilius* are scored as (1) based on the circular/ovoid cross section of the first incisors, even though it is unknown if these teeth were bicolumnar in early wear stages. Finally, *Miocochilius* was scored as (1), based on the circular cross section of i1, but it should be noted that i2 has a somewhat intermediate morphology between character state (0) and (1). Instead of dividing this into two different characters, we thought it most prudent to simply score *Miocochilius* as (1) overall.

20. **Procumbence of lower incisors, canine, and p1**: (0) absent; (1) present.

This is character 29 in Reguero *et al*., 2003, but is scored differently for 2 taxa. *Archaeophylus*, which was scored as (0) for this character by Reguero *et al*. (2003), was left as unknown (?) in this study, since the lower, anterior dentition of *Archaeophylus* is only known from isolated teeth. Also, although Reguero *et al*. (2003) score *Progaleopithecus* as (0) for this character, our own observations suggest that the procumbence of the anterior dentition in AMNH 29603 (*Progaleopithecus*) is notable, and at least as strong as that observed in various specimens of *Protypotherium* and *Cochilius*. Hence, we have scored this character as (1) for *Progaleopithecus*. *Plagiarthus* is scored following the dataset in Reguero *et al*., 2003, since we did not have access to any specimens of *Plagiarthus proavunculus*.

21. **i3 size**: (0) i3 > i2; (1) reduced (i3 < i2).

This is character 19 in Hitz *et al*., 2006, in which this character is scored as (?) for *Brucemacfaddenia*. According to the description of the anterior dentition in Hitz *et al*., 2006 (pg. 453), although i1-2 are broken, it is clear that i3 is larger than i2. As such, herein this taxa is scored as (0) for this character.

22. **size of canine and p1**: (0) subequal in size to p2; (1) notably smaller than p2, but part of a series of size increase from i1-p1; (2) highly reduced or absent.

This is similar to character 21 in Hitz *et al*., 2006, and character 9 in Reguero *et al*., 2003. However, this character description has been rewritten for greater clarity, and therefore various taxa are scored differently. *Plagiarthus* is scored following the description in Reguero, 1999, and the dataset in Reguero *et al*., 2003, since we did not have access to any specimens of *Plagiarthus proavunculus*.

23. **c-p1 diastema**: (0) absent; (1) present.

This is character 21 in Hitz *et al*., 2006, and similar to character 17 in Reguero *et al*., 2003. Although Reguero *et al*. (2003) score *Protypotherium* as (1), we agree with Hitz *et al*. (2006) that *Protypotherium* should be scored as (0) for this character. Although there are some specimens of *Protypotherium* with a very slight space between c and p1, we don't

consider this significant enough to be called a diastema. *Plagiarthus* was scored following the dataset of Reguero *et al*. (2003).

24. **p2-4 talonid development and relative size**: (0) p2 talonid small or absent, p3-4 distinct but smaller than trigonids; (1) p2-3 talonids distinct and smaller than or subequal to trigonids, p4 talonid subequal to trigonid; (2) p2 talonid distinct and smaller than or subequal to trigonid, p3 and p4 talonid larger than trigonid.

This is similar to character 23 in Hitz *et al*., 2006 and character 14 in Reguero *et al*., 2003. This character has been rewritten for clarity, resulting in several scoring differences from previous studies.

25. **p3 molarization**: (0) premolariform; (1) molariform.

This is character 8 in Reguero *et al*., 2003, and similar to character 27 in Hitz *et al*., 2006. We decided not to include p4, as in Hitz *et al*., 2004 (character 27), since determining the difference between "approaching molariform" and "molariform" for this tooth proved ambiguous. Neither of these previous studies defines molariform. Here we define molariform as "similar in both size and morphology to m1" and premolariform as "more similar in size and/or morphology to p2 rather than to m1."

26. **p3-4 crown morphology**: (0) narrow labial sulcus, more posteriorly oriented lingual sulcus; (1) bilobed, persistent labial and lingual sulci directly opposite each other.

This is character 24 in Hitz *et al*. 2006. *Federicoanaya* was scored as (1), following specimen descriptions by Hitz *et al*. (2008), whereas Hitz *et al*. (2006) scored this taxon as (?) for this character.

27. **metacristid on p4-m3**: (0) well developed – forming a distinct and persistent feature separated from the rest of the trigonid by a deep sulcus; (1) present, but with wear merges considerably with the rest of the trigonid, separated only by a shallow sulcus; (2) absent.

This is character 5 in Reguero *et al*., 2003. The character description was rewritten to be more strictly applicable to the taxa included in this study.

28. **m1-3 talonid development and relative size**: (0) m1 talonid subequal to or slightly smaller than trigonid, m2 talonid subequal to or slightly larger than trigonid, m3 talonid larger than trigonid; (1) all talonids larger than trigonids.

This is character 25 in Hitz *et al*., 2006.

29. **lingual sulcus of trigonid on lower molars**: (0) present; (1) absent.

This is character 15 in Reguero *et al*., 2003.

30. **shape of m2-3 trigonid**: (0) quadrangular, with broad, flat anterior margin; (1) triangular, with narrow anterior margin; (2) semi-circular, with broad, rounded anterior margin.

This is similar to character 28 in Hitz *et al*., 2006, and character 2 in Reguero *et al*., 2003. Herein we limit this character to m2-3 (instead of all the molars, as in previous studies), having observed that the shape of the m1 trigonid can differ from the shape of m2-3 trigonids (e.g., *Protypotherium* and Ineteratheriinae gen *et* sp. *nov*. B). Also, the character descriptions were rewritten for greater clarity. As such, numerous taxa are scored differently than in previous studies.

31. **lingual sulcus on m3 talonid**: (0) salient; (1) faint or absent.

*Plagiarthus* was scored as (0), since this ridge remains salient through most wear stages, and only becomes faint with extreme wear (Reguero, 1999).

32. **labial sulcus on m3 talonid**: (0) faint or absent; (1) salient.

This is similar to character 29 in Hitz *et al*., 2006, and character 26 in Reguero *et al*., 2003, but the character descriptions were rewritten for greater clarity. We score

*Protypotherium* as (0) for this character, at odds with both previous studies. It is our observation that this sulcus, if present, is quite faint, and not as pronounced as it is in *Miocochilius* and *Progaleopithecus*. Also, we scored *Johnbell* based on the description and figures available in Hitz *et al*., 2006.

33. **Nasofrontal suture shape**: (0) nearly straight transversely; (1) nasal trends posteriorly from the median; (2) nasal trends posteriorly from the median but is jagged with small posteriorly projecting process.

This is character 32 in Hitz *et al*., 2006, but includes one less character state, since we do not include *Colbertia* as an outgroup in this study.

34. **Descending process on zygoma**: (0) small or absent; (1) large.

This is similar to character 33 in Hitz *et al*., 2006, and character 25 from Reguero *et al*., 2003. We agree with Reguero *et al*. (2003) that *Cochilius* is characterized by a large descending process, and *Plagiarthus* is characterized by a small descending process, but note that these taxa are scored differently by Hitz *et al*. (2006).

35. **Dorsal-posterior maxillary process**: (0) dorsal process present but is not excluded from orbit rim; (1) dorsal process present and is excluded from orbit margin by an anteriorly projecting sliver of frontal.

This is character 34 in Hitz *et al*., 2006.

36. **Rostrum length**: (0) rostrum short compared to anteroposterior length of skull, <35% of total cranium length; (1) modest lengthening of rostrum, ≥35% of total cranium length.

This is character 35 in Hitz *et al*., 2006.

37. **Angle of zygoma with face, at attachment site**: (0) steep angle (>45° and <90°); (1) perpendicular (90°).

This is character 36 in Hitz *et al*., 2006, but includes one less character state, since we do not include *Colbertia* as an outgroup in this study.

38. **Dorsal-posterior process on external premaxillary**: (0) absent; (1) present.

This is character 38 in Hitz *et al*., 2006. Since *Notopithicus* is scored as "absent," we make "absent" the basal character state (0), whereas "absent" is the derived condition (1) in Hitz *et al*., 2006.

39. **Palatine notch position**: (0) reaches mid to anterior M3 region; (1) reaches posterior M3 region.

This is character 39 in Hitz *et al*., 2006.

40. **Posterior bulla**: (0) adjacent to paraoccipital process; (1) posterior bulla laps up onto paraoccipital process.

This is character 40 in Hitz *et al*., 2006.

Appendix 2.2: Character taxon matrix for Interatheriinae.

For polymorphic taxa, a letter is used to represent multiple states: ‘A’ indicates character states 0 and 1.

| | | | | | 5 | | | | | | 10 | | | | 15 | | | | | 20 | | | | | 25 | | | | | 30 | | | | | 35 | | | | | 40 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Notopithecus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Johnbell* | ? | ? | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | ? | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? | ? | ? |
| *Ignegena* | ? | ? | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | ? | 0 | ? | ? | ? | 0 | ? | ? | 0 | ? | 0 | ? | 0 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Eopachyrucos* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 1 | 1 | 1 | ? | 1 | ? | 0 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Proargyrohyrax* | ? | ? | ? | ? | ? | ? | ? | 0 | ? | ? | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | ? | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | ? | ? | 0 | ? | ? | ? | ? |
| *Santiagorothia* | ? | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | ? | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 1 |
| INT C | ? | ? | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Brucemacfaddenia* | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | ? | 1 | 0 | 0 | ? | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Plagiarthus* | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | ? | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 1 | ? | 1 | ? | 1 | 1 |
| *Archaeophylus* | ? | ? | ? | ? | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | ? | ? | ? | ? | ? | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 1 | 0 | ? | 0 | ? | ? | 1 | ? | ? | ? |
| *Interatherium* | 1 | 1 | ? | 0 | A | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| *Cochilius* | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 |
| INT B | 1 | 0 | ? | 0 | ? | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Federicoanaya* | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 1 | 0 | 0 | ? | ? |
| INT A | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 1 | 0 | 1 | 0 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | ? | ? | ? | ? | ? | ? | ? | ? |
| *Protypotherium* | A | 0 | A | 1 | A | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 1 | 0 | 1 | 0 | 1 |
| *Progaleopithecus* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | ? | ? | ? | ? | ? | ? | ? | ? |
| *Miocochilius* | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 2 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 |

Appendix 2.3: Interatheriid taxa, references consulted, and specimens used for the phylogenetic analysis.

- *Notopithecus adapinus* Ameghino, 1897: Simpson, 1967
- *Cochilius volvens* Ameghino, 1902: Simpson, 1932b; various specimens in AMNH, MACN, and MLP collections
- *Cochilius fumensis* Simpson, 1932a: Simpson, 1932a; AMNH 29551
- *Brucemacfaddenia boliviensis* Hitz *et al*., 2008: Hitz *et al*. 2008
- *Federicoanaya sallaensis* Hitz *et al*., 2008: Hitz *et al*. 2008
- *Ignigena minisculus* Hitz *et al*., 2006: Hitz *et al*., 2006
- *Johnbell hatcheri* Hitz *et al*., 2006: Hitz *et al*., 2006
- *Protypotherium australe* Ameghino, 1887: Sinclair, 1909; Tauber, 1996; various specimens in AMNH, MACN, YPM-PU, and MLP collections
- *Protypotherium praerutilum* Ameghino, 1887: Sinclair, 1909; Tauber, 1996; various specimens at the AMNH, MACN, YPM-PU, and MLP
- *Protypotherium attenuatum* Ameghino, 1887: Sinclair, 1909; Tauber, 1996; various specimens at the AMNH, MACN, YPM-PU, and MLP
- *Miocochilius anomopodus* Stirton, 1953: Stirton, 1953; UCMP 39248; AMNH 45882
- *Miocochilius federicoi* Croft, 2007: Croft, 2007
- *Interatherium robustum* Ameghino, 1887: Sinclair, 1909; various specimens in AMNH, MACN, and MLP collections
- *Interatherium extensum* Ameghino, 1887: Sinclair, 1909; various specimens in AMNH, MACN, and MLP collections
- *Santiagorothia chiliensis* Hitz *et al*., 2000: Hitz *et al*., 2000; various specimens at the AMNH
- *Proargyrohyrax curanderensis* Hitz *et al*., 2000: Hitz *et al*., 2000
- *Eopachyrucos pliciferus* Ameghino, 1901: Hitz *et al*., 2000
- *Eopachyrucos ranchoverdensis* Reguero *et al*., 2003: Reguero *et al*., 2003
- *Plagiarthus clivus* (= *Argyrohyrax proavus*) Ameghino, 1887: MACN-A 52-472, MACN-A 52-474, MACN-A 52-475.
- *Plagiarthus proavunculus* (= *Argyrohyrax proavunculus*) (Reguero 1999): Reguero, 1999. Specimen descriptions of this taxon in Reguero, 1999 were especially important for scoring the anterior lower dentition of *Plagiarthus*.
- *Archeophylus patrius* Ameghino, 1897: MACN-A 52-483, MACN-A 52-484, and MACN-A 52-485; a few characters of the lower premolars were scored based on descriptions in Reguero, 1999.
- *Progaleopithecus tourneri* Ameghino, 1904: Hitz *et al*., 2006; AMNH 29603.

Appendix 2.4: *Protypotherium* species and junior synonyms

- *Protypotherium antiquum* Ameghino, 1885
  - Ameghino (1885) originally described this species on the basis of a mandibular symphysis and a partial mandible bearing p4-m3. The symphysis has not been located, but the mandible has been identified as ZMUC ZMK 21/1877, which should be regarded as the holotype.
  - Interatheriinae *incertae sedis*. See taxonomic note 1 in Remarks section of *Protypotherium* Systematic Paleontology.
- *Protypotherium australe* Ameghino, 1887b
  - Ameghino (1887b) originally described this species on the basis of a mandible (partial?) with at least p1-m3. It is unknown which specimen(s) this refers to. A more complete description (Ameghino, 1889) refers to the existence of numerous specimens, and several specimens are illustrated (plate 14, figs. 9-11 and 14-18). Fernicola (2011) identified two of these illustrated specimens: MACN-A 550 (partial maxilla bearing P4-M3; plate 14, figs. 17 and 17a in Ameghino, 1889) and MACN-A 530 (partial mandible bearing p3-m3; plate 14, figs. 18 and 18a in Ameghino, 1889). These specimens were not examined in this study. Also note that there are several specimens at the MACN that are labeled as syntypes of *P. australe*. Presumably, these were selected by Ameghino after 1889, or by a later researcher. These specimens include: MACN-A 3882 (nearly complete skull, with complete dentition except for missing left I1-3, missing right I1 and partial left I2); MACN-A 3883 (partial maxilla bearing P1-M3); and MACN-A 3884 (partial mandible bearing right i1-3 and p2-m3; and left i1-3).
  - We consider this taxon valid, and have suggested it should be the genotype of *Protypotherium*. See taxonomic note 1 in Remarks section of *Protypotherium* Systematic Paleontology. Also, see text for the distinguishing characters between *P. australe* and *P. praerutilum*.
- *Protypotherium praerutilum* Ameghino, 1887b
  - Ameghino (1887b) originally described this species on the basis of a (partial?) mandible with at least p1-m3. It is unknown which specimen(s) this refers to. A more complete description (Ameghino, 1889) lacks reference to any type specimens, but several specimens are illustrated (plate 14, figs. 6-8 and 12-13), including MACN-A 1081 (partial skull bearing left I1-M3 [fragmentary M1-2] and right P1-M3 [fragmentary P2, M1]; plate 14, figs. 6, 6a, 6b in Ameghino, 1889) and MACN-A 1082 (partial mandible bearing right i1-m3 and fragments of left i1-3; plate 14, figs. 7, 7a in Ameghino 1889). Both specimens are labeled as types at the MACN. Also labeled as a type is MACN-A 1083 (partial left mandible bearing m1-3; almost certainly pertaining to the same individual as specimen MACN-A 1082).
  - We consider this taxon valid (see text for emended diagnosis).
- *Protypotherium attenuatum* Ameghino, 1887b
  - Ameghino (1887b) originally described this species on the basis of a mandible (partial?) with at least p3-m3, and several upper teeth in series (identity of upper teeth unspecified; specimens unknown). A slightly more complete description (Ameghino, 1889) includes illustrations of two specimens (plate 14, figs. 20, 20a, 21). MACN-A 524 (partial maxilla bearing P2-M3; labeled as a type specimen) is very similar to the specimen illustrated in Plate 14, Figure 21 (Ameghino, 1889),

except that MACN-A 524 does not possess P1. Therefore, MACN-A 524 may have been damaged and lost P1, or it could be a different specimen later chosen as the type. Fernicola (2011) also suggests that MACN-A 627 is illustrated in Ameghino, 1899; presumably this specimen corresponds to plate 14, figs. 20 and 20a. This specimen was not examined in the present study.

- We tentatively consider this taxon valid. We note, however, that the character most consistently used to diagnose *P. attenuatum* – its relatively small size compared to *P. australe* and *P. praerutilum* (Ameghino, 1887b, 1889; Sinclair, 1909; Tauber, 1996) – can be quite difficult to determine in practice, since there appears to be considerable overlap in size between *P. attenuatum* and *P. praerutilum* (see tables 2.5-6 and figs. 2.7-8). However, as Ameghino (1887b, 1889) originally suggests, another potentially diagnostic character is the highly curved upper tooth-row (seen primarily in P2-M3) of *P. attenuatum*. This curvature has not been consistently used to diagnose the species (Sinclair, 1909; Tauber, 1996), even though it is characteristic of two taxa – *Protypotherium globosum* and *Patriarchus icochiloides* – that both Sinclair (1909) and Tauber (1996) consider junior synonyms of *Protypotherium attenuatum*. Furthermore, several more recently proposed diagnostic characters of *P. attenuatum* are of dubious value. For example, Sinclair (1909) suggests that, through synonymy with *P. globosum*, *P. attenuatum* is distinguished by "the marked convexity of the brain-case just posterior to the fronto-parietal suture," but we note that similar concavity is observed in much larger specimens of *P. australe* (e.g., MACN-A 37). Tauber (1996) provides several additional diagnostic characters for *P. attenuatum*, some of which we consider of potential value (e.g., short rostrum and relatively broad palate), but relatively few specimens allow this morphology to be examined directly. Furthermore, several diagnostic characters proposed by Tauber (1996) are either ambiguously qualitative, or known to be variably present within *P. australe* and *P. praerutilum*. Finally, we recognize that these difficulties may reflect an underlying issue: *P. paerutilum* and *P. attenuatum* may simply represent end-members of intraspecific variation, and should not be considered distinct taxa. In this case, *P. praerutilum* should have priority – both taxa are originally described by Ameghino (1887b), but the description of *P. praerutilum* appears first. MACN-A 4044 ("*Patriarchus diastematus*") may be pertinent to this discussion (see below).

- *Protypotherium obstructum* Ameghino, 1888
  - Ameghino (1888) described this species on the basis of a single tooth, either p3 or p4, from Monte Hermoso. MACN-A 1677, a right p3 or p4 labeled as the type, matches the original description.
  - This specimen was not treated in the revisions of Sinclair (1909) and Tauber (1996). We note that while the general shape of the tooth (especially the relatively small talonid that abuts closely against the trigonid) is similar to the premolars of *Protypotherium*, MACNA-A 1677 possesses two unique characters: 1) the anterior margin of the trigonid is broader and less rounded than in any specimens of *Protypotherium* examined; and 2) the labial sulcus between the trigonid and talonid is positioned more anteriorly than in *Protypotherium*. These observations, coupled with the fact that this taxon was established on the

basis of a single tooth, lead us to regard MACN-A 1677 as Interatheriinae *incertae sedis*, cf. *Protypotherium*.

- *Protypotherium claudum* Ameghino, 1889
  - Ameghino (1889) described this species on the basis of a right mandibular fragment bearing p2-m2. MACN-A 551, which is labeled as the type specimen of *P. claudum*, matches both the original description (Ameghino, 1889) and the accompanying illustration (Plate 14, Figures 22, 22a).
  - Sinclair (1909) did not examine material of this taxon, and therefore lists it as "Typotheria *incertae sedis*." Tauber (1996) synomymized *P. claudum* with *P. australe*. We note that p3 of MACN-A 551 is unique among all *Protypotherium* specimens examined in possessing 1) a talonid that projects further labially and 2) a labial sulcus between the talonid and trigonid that is broader and more medially located. While this observation may aid future taxonomic revisions, we recognize Tauber's (1996) synonymization as presently valid.
- *Patriarchus palmidens* Ameghino, 1889 (synonymized with *Protypotherium australe* by Sinclair [1909])
  - Ameghino (1889) originally described this species on the basis of at least two specimens – a mandibular symphysis bearing left i1-2 and right i1-p1, and a mandibular fragment bearing (right?) i1-2. These specimens are illustrated in the same publication (plate 15, figs. 2, 2a-c). To the best of our knowledge, these specimens have not been identified. A more complete specimen housed at the MACN is labeled as the type of *Protypotherium palmidens*. This specimen, MACN-A 37, includes a nearly complete skull bearing left I3-M3 and right I2-M3, and a partial right mandible bearing p1-m3. Presumably, MACN-A 37 was selected as a type by Ameghino after 1889, or by a later researcher.
  - We agree with Sinclair (1909) and Tauber (1996) that *Patriarchus palmidens* is synonymous with *Protypotherium australe*.
- *Protypotherium globosum* Ameghino, 1891 (synonymized with *Protypotherium attenuatum* by Sinclair [1909])
  - Ameghino (1891) originally described this species on the basis of at least one reasonably complete skull. MACN-A 4049 (nearly complete skull bearing right I3-M3 and left C-M3), which is labeled as the type, almost certainly corresponds to this original description.
  - We agree with Sinclair (1909) and Tauber (1996) that *Protypotherium globosum* is synonymous with *Protypotherium attenuatum*. It noteworthy that MACN-4049 is characterized by a strongly curved upper tooth-row, which may be a useful diagnostic character of *P. attenuatum*.
- *Protypotheirum convexidens* Ameghino, 1891 (synonymized with *Protypotherium praerutilum* by Sinclair [1909])
  - Ameghino (1891) originally described this species on the basis of at least one maxillary fragment bearing P3-M2 in series, but a type is not identified. Although four specimens of *P. convexidens* were examined (MACN-A 9643, MACN-A 4053, MACN-A 4054, MACN-A 4055), none of these specimens is labeled as the type, and none bears just P3-M2 (although MACN-A 9643, the most complete of these specimens, does bear P2-M2). Moreover, all of these

specimens are somewhat smaller than the specimen(s) referred to in Ameghino's (1891) original description.
    - Sinclair (1909) lists ?*Protypotherium convexidens* as a junior synonym of *Protypotherium praerutilum*, and Tauber (1996) follows this convention (even including the question mark). Considering the specimens examined (see above), we understand the basis of this synonymy, but we suggest that the uncertainty stems from ambiguity in Ameghino's (1891) original description – an error in this publication results in a nonsensical diagnosis of *Protypotherium convexidens*. Considering this descriptive error, the lack of a type specimen, and the relatively small size (compared to the original description) of the four specimens examined, we consider *Protypotherium convexidens* a *nomen nudum*.
- *Protypotherium diversidens* Ameghino, 1891
    - Ameghino (1891) originally described this species on the basis of at least one maxillary fragment, but a type is not identified. Ameghino (1891) indicates that the length of P2-M2 is 24 mm, but also that the size of this specimen is "relatively small" (translation from Spanish). A P2-M2 length of 24 mm, however, would correspond to a medium-sized specimen of *Protypotherium* (near the upper size range of *P. praerutilum*). We note that MACN-A 4052, which is labeled as the type specimen, bears right P2-M3 in series, and that the length of these teeth is 23.7 mm. Furthermore, this specimen certainly exhibits the diagnostic features indicated by Ameghino (1891) (see below). As such, we conclude that Ameghino's (1891) original description contains a typographical error – instead of "P2-M2" the measurement should read "P2-M3" – and that MACN-A 4052 does indeed represent the type.
    - Sinclair (1909) was not able to examine material of this taxon, and therefore lists it as "Typotheria *incertae sedis*." Tauber (1996) does not list or discuss *P. diversidens* in his revision of *Protypotherium*. We note that MACN-A 4052 possesses several unique characters that make assignment to *Protypotherium* untenable: 1) the labial face of the premolars bear a salient, v-shaped sulcus that becomes broader towards the crown (a character identified by Ameghino [1891] as diagnostic for the taxon); we have not observed such strongly v-shaped labial sulci in any specimens of *Protypotherium* (or any interatheriid taxa, for that matter); 2) the M2 is notably larger than M1; whereas in *Protypotherium* M1 is the largest tooth; 3) the P3-4 parastyles are very large, similar to *Miocochilius* and *Federicoanaya*; whereas the P3-4 parastyles of *Protypotherium* are relatively short. Accordingly, we consider MACN-A 4052 Interatheriinae *incertae sedis*.
- *Protyptherium compressidens* Ameghino, 1891 (synonymized with *Protypotherium praerutilum* by Sinclair [1909])
    - Ameghino (1891) originally described this species on the basis of at least a maxillary fragment bearing P3-M3 in series, but a type is not identified. MACN-A 4029 (maxillary fragment bearing P3-M3) matches the original description (and measurements therein) perfectly. Two specimens at the MACN are labeled as types: MACN-A 4029 (which we recognize as the holotype) and MACN-A 4030 (corresponding p1-m3; recognized herein as a paratype).

- Sinclair (1909) and Tauber (1996) synonymized this taxon with *Protypotherium australe*. Although MACNA-4029 and MACN-A 4030 possess all the diagnostic characters of *Protypotherium* (see Systematic Paleontology herein), these teeth are markedly more compressed (labiolingually narrow) than any *Protypotherium* specimens examined in this study (see fig. 2.7 and table 2.6). We suggest that Sinclair's (1909) synonymization is not warranted and that the taxon *Protypotherium compressidens* is valid.

- *Patriarchus furculosus* Ameghino, 1891 (synonymized with *Protypotherium australe* by Sinclair [1909])
  - Ameghino (1891) originally described this species on the basis of at least a partial skull (the diagnosis primarily involves the shape of the frontals and nasals), and a nearly complete lower tooth-row. A type was not identified, and no specimen matching this description has been examined. MACN-A 3970 (partial mandible bearing p2-m2) and MACN-A 3972 (maxillary fragments bearing P2-M3) are labeled as types, and several other specimens in the MACN-A collections are labeled *Protypotherium furculosus*. None of these specimens include the nasals and frontals, which are diagnostic of the taxon.
  - Sinclair (1909) and Tauber (1996) synonymized this taxon with *Protypotherium australe*. Based on the specimens we examined, the large size indicated by Ameghino's (1891) description, the observed variability within *Protypotherium*, and the absence of Ameghino's (1891) proposed diagnostic character (elongated frontals that anteriorly form a wedge between the nasals), we accept this synonymization.
- *Patriarchus distortus* Ameghino, 1891 (synonymized with *Protypotherium distortum* by Ameghino (1894); synonymized with *Protypotherium australe* by Sinclair [1909])
  - Ameghino (1891) originally described this species on the basis of at least a reasonably complete skull, but he identified no type specimen. We found no specimen labeled as the type, but we did examine several specimens labeled *P. distortus*. Although aspects of these specimens match the original description (Ameghino, 1891), none of these specimens included a reasonably complete skull, and therefore do not correspond to the specimen(s) used to fully diagnose this taxon.
  - We agree with Sinclair (1909) and Tauber (1996) that *Patriarchus distortus* is synonymous with *Protypotherium australe*.
- *Patriarchus rectus* Ameghino, 1891 (synonymized with *Protypotherium attenuatum* by Sinclair [1909])
  - Ameghino (1891) originally described this species on the basis of at least a partial skull and lower dental series, but he identified no type specimen. Three specimens are labeled as the types: MACN-A 4005 (partial maxilla with right P1-M3), MACN-A 4006 (partial maxilla with left M1-3), and MACN-A 4007 (partial mandible with i3-m3). These specimens might correspond to the original description, but only if the upper maxillary fragments originally corresponded to a more complete skull (Ameghino [1891] indicated the interorbital width of the frontals). Besides the lack of frontals, all other aspects of these specimens match Ameghino's (1891) description.

- Sinclair (1909) and Tauber (1996) synonymized this taxon with *Protypotherium attenuatum*. This decision was almost certainly based on the small size of the specimens examined, but it can be difficult to distinguish between *P. attenuatum* and *P. praerutilum* based on size alone (see text, figs. 2.7-8, and tables 2.5-7). The specimens examined in this study (MACN-A 4005, MACN-A 4006, MACN-A 4007) clearly pertain to a juvenile, and are in some respects slightly smaller than specimens regarded as *P. praerutilum*, but we suggest that this small size may simply reflect one end of a continuous range of variation for *P. praerutilum* (see figs. 7-8 and tables 5-7). In addition, we suggest that a highly curved upper tooth-row may be an important diagnostic character of *P. attenuatum*, as recognized in Ameghino's (1887b) original description. Both the original description of *Patriarchus rectus* (Ameghino, 1891) and our examination of the possible type specimens clearly indicate a relatively straight tooth-row. For these reasons, we suggest that *Patriarchus rectus* is more appropriately synonymized with *Protypotherium praerutilum*.

- *Patriarchus diastematus* Ameghino, 1891
  - Ameghino's (1891) original description undoubtedly corresponds to MACN-A 4044 (partial palate bearing left and right P2-M3).
  - Sinclair (1909) was not able to examine material of this taxon, and therefore lists it as "Typotheria *incertae sedis*." Tauber (1996) does not list or discuss *Patriarchus diastematus* in his revision of *Protypotherium*. Ameghino's (1891) principal diagnostic feature for this taxon is the cylindrical P1 separated from P2 by a small diastema, but we note that while MACN-A 4044 matches this description, both P1s are broken and can only be observed within the alveoli. This specimen appears to possess cheek-teeth that are strongly curved (slightly more pronounced along the right tooth-row), which we have suggested may be diagnostic of *P. attenuatum*. However, MACN-A 4044 possesses larger teeth than any specimen labeled as (or synonymized with) *P. attenuatum.* This suggests that MACN-A 4044 could potentially represent 1) a large *P. attenuatum*; 2) an average-sized *P. praerutilum* with an abnormally curved tooth-row; or 3) a different taxon (*P. diastematus*) with a combination of features seen in *P. paerutilum* and *P. attenuatum*. Lastly, 4) *P. paerutilum* and *P. attenuatum* may not, in fact, represent distinct species, but might instead reflect end-members in a continuum of intraspecific variation, with MACN-A 4044 "bridging" this apparent gap of size and morphology.

- *Patriarchus leptocephalus* Ameghino, 1891 (synonymized with *Protypotherium praerutilum* by Sinclair [1909])
  - Ameghino (1891) originally described this species on the basis of at least a reasonably complete skull, but did not identify a type. This description almost certainly corresponds to MACN-A 3989 (nearly complete skull bearing P4-M3 and left P3-M3; several of these teeth are broken), which is labeled as the type specimen. Two other specimens are labeled as "second types": MACN-A 3990 (partial left maxilla and premaxilla bearing I1-M3), and MACN-A 3991 (partial left mandible i2-m3).

- Sinclair (1909) synonymized this taxon with *Protypotherium praerutilum*, but Tauber (1996) does not list or discuss *Patriarchus leptocephalus* in his revision of *Protypotherium.* We accept Sinclair's (1909) synonymization.

- *Patriarchus altus* Ameghino, 1891 (synonymized with *Protypotherium australe* by Sinclair [1909])
  - Ameghino (1891) originally described this species on the basis of at least a reasonably complete skull with nearly complete dentition, but did not identify a type. MACN-A 4001 (nearly complete skull bearing right I1-M3 [broken I1 and P2] and left P1-M3 [M3 broken]), which is labeled as the syntype, matches most aspects of the original description. However, Ameghino (1891) provides several measurements that apparently correspond to a specimen that is slightly larger than MACN-A 4001. Two additional specimens are labeled as syntypes: MACNA-A 3999 (partial skull bearing left and right C-M3) and MACN-A 4000 (partial mandible bearing left p4-m3 and several more teeth that remain encased in matrix). Neither of these "syntypes" appear to correspond to the specimen(s) originally described by Ameghino (1891).
  - Sinclair (1909) and Tauber (1996) synonymized this taxon with *Protypotherium australe*. Although Ameghino's (1891) original description may not correspond to any of the specimens examined, there is a general similarity between these specimens and the original description. Based on this material, we accept the synonymy of this taxon and *Protypotherium australe*.
- *Protypotherium lineare* Ameghino, 1894 (synonymized with *Protypotherium australe* by Sinclair [1909])
  - Ameghino (1891) originally described this species on the basis of at least a partial mandible bearing p1-m3, but did not identify a type. Two specimens at the MACN are labeled as types: MACN-A 4038 (partial right mandible bearing p2-m1) and MACN-A 4039 (partial left mandible bearing p3-m2). Although these specimens certainly do not correspond to the original description, they exhibit some of the characters referred to in Ameghino's description.
  - Sinclair (1909) and Tauber (1996) synonymized this taxon with *Protypotherium australe*. Although Ameghino's (1891) original description does not correspond to any of the specimens examined, there is a general similarity between these specimens and the original description. Accordingly, we accept the synonymy of this taxon with *Protypotherium australe*.
- *Patriarchus icochiloides* Ameghino, 1894 (synonymized with *Protypotherium attenuatum* by Sinclair [1909])
  - Ameghino (1891) originally described this species on the basis of at least a partial upper tooth-row and partial lower mandible bearing p1-m3, but did not identify a type. MACNA-4021 (partial right maxilla bearing P2-M3; P3 and M3 broken) and MACN-4022 (partial right mandible bearing p4-m3, and broken p2-3), both labeled as types, match nearly every aspect of the original description, except that the mandible lacks p1. We suspect the anterior portion of the mandible may have been broken.
  - We agree with Sinclair (1909) and Tauber (1996) that *Patriarchus icochiloides* is synonymous with *Protypotherium attenuatum*. As may be diagnostic of *P. attenuatum*, MACN-4021 is characterized by a strongly curved upper tooth-row.

- *Protypotherium martini* Lane, 1927
  - Holotype: No. 19 (collector's No. 69) of the Patagonian collection, Museum of the University of Kansas, Department of Vertebrate Paleontology (partial left maxilla and premaxilla bearing P2-M3 and alveoli of I1-P2, and fragment of left frontal).
  - Although we have not directly examined these materials, we did compare several aspects of the original diagnosis (Lane, 1927) to dozens of *Protypotherium* specimens (at the MLP, MACN, YPM-PU, and AMNH). This comparison suggests that *P. martini* should be synonymized with *P. australe*. For a more complete discussion, see taxonomic note 4 in the Remarks section of *Protypotherium* Systematic Paleontology.
- *Protypotherium distinctum* Cabrera and Kraglievich, 1931
  - Holotype: MLP 12-2178 (partial right maxilla bearing P3-M3). We were unable to locate this specimen.
  - While we have not examined any material of *P. distinctum*, we note that several characters identified as diagnostic for this taxon (Cabrera and Kraglievich, 1931; Bond and Lopez, 1996) may be variably present among specimens of *P. australe*, *P. praerutilum*, and/or *P. attenuatum*.
- *Protypotherium minutum* Cabrera and Kraglievich, 1931
  - Holotype: MLP 12-2176 (partial maxilla and mandible). We note that MLP 12-2177 is also labeled as the holotype, and includes the same specimen description as MLP-2176. Perhaps one of these specimen numbers is intended to apply to the maxilla, and the other to the mandible. Although we found these labels, we were unable to locate the specimens.
  - While we have not examined any material of *P. minutum*, we note that several characters identified as diagnostic for this taxon (Cabrera and Kraglievich, 1931; Bond and Lopez, 1996) may be variably present among specimens of *P. australe*, *P. praerutilum*, and/or *P. attenuatum*.
- *Protyptherium minor* Bordas, 1939
  - Holotype: MACN 11742 (partial skull bearing left P2-M3 and right P2-M1, along with fragments of right M2-3 and fragments of anterior teeth that are difficult to identify).
  - MACN 11742 possess molariform premolars, with strongly developed paralophs that are similar in size to the metalophs, giving the occlusal surface of the premolars a generally rectangular outline. This is incompatible with all diagnoses of *Protypotherium* (e.g., Ameghino, 1889; Sinclair, 1909; herein), since the genus is characterized by premolars that are sub-triangular in occlusal outline, with relatively small paralophs. We suggest that MACN 11742 (the holotype and only specimen of "*P. minor*") should be considered Interatheriinae *incertae sedis*, cf. *Interatherium*.

Appendix 2.5: *Protypotherium* specimen measurements.
Abbreviations: Pal. = palate; md = mesiodistal; ll = labiolingual

| Taxon | Specimen No. | I1 md | I2 md | I3 md | M1 md | M1 ll | M2 md | M2 ll | M3 md | M3 ll | Pal. l | Pal. w |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *P. australe* | MACN-A3882 | | | | 8.8 | 6.2 | 8 | 5.6 | 7.4 | 4.4 | 53.2 | 24.1 |
| *P. australe* | MACN-A 3883 | | | | 8.1 | 5.1 | 7.3 | 4.9 | 7.3 | 4.2 | | |
| *P. australe* | MACN-A 37 | 6.7 | 5.1 | 4.7 | 8.1 | 5.1 | 7.46 | 4.7 | 6.5 | 4.32 | 53.6 | 22.2 |
| *P. australe* | MACN-A 3999 | | | | 8.0 | 5.3 | 7.14 | 4.9 | 7.6 | 4.26 | | |
| *P. australe* | MACN-A 4001 | 5.9 | 4.6 | 4.75 | 8.3 | 5.4 | 7.3 | 4.96 | 7.3 | 4.1 | 54.3 | 22.8 |
| *P. australe* | MACN-A 3970 | | | | 8.5 | 5.4 | 7.58 | 4.9 | 7.42 | 4.3 | | |
| *P. australe* | MACN-A 3977 | | | | 9.0 | 5.3 | 8.3 | 5.0 | 7.44 | 4.14 | | |
| *P. australe* | MACN-A 3984 | | | | 9.2 | 5.08 | 7.1 | 4.72 | | | | |
| *P. australe* | MACN-A 39 | 6.9 | 5.3 | 4.86 | 8.2 | 5.4 | 7.22 | 4.9 | | | 54.5 | 23.8 |
| *P. australe* | MACN-A 3885 | 6.65 | 4.9 | 4.84 | 8.1 | 5.2 | 7.65 | 4.62 | 7.5 | 3.94 | | |
| *P. australe* | MACN-A 3913 | | | | 8.4 | 5.3 | 7.52 | 4.8 | 7.16 | 3.76 | | |
| *P. australe* | MACN-A 3912 | | | | 8.22 | 5.5 | 7.6 | 4.86 | 6.6 | 4 | | |
| *P. australe* | MACN-A 3977 | | | | 8.9 | 5.24 | 7.86 | 4.92 | 7.34 | 4.32 | | |
| *P. australe* | MACN-A 9644 | 5.9 | 4.9 | 4.84 | | | | | | | | |
| *P. australe* | MACN-A 9534 | 6.13 | 4.5 | 4.53 | 8.2 | 5.04 | 7.24 | 4.73 | 6.72 | 3.87 | 54.4 | 22.4 |
| *P. australe* | MACN-A 9565 | 6.35 | 5.39 | 5.22 | 8.38 | 5.12 | 7.47 | 4.96 | 7.41 | 4.15 | | |
| *P. australe* | MLP 12-2026 | | | | 8.3 | 5.1 | | | | | | |
| *P. australe* | MLP 12-2792 | | | | 8.2 | 5.6 | | | | | | |
| *P. australe* | MLP 84-III-1-88 | | | | 8.94 | 5.54 | | | | | | |
| *P. australe* | MLP 26-IV-25-9 | | | | 8.45 | 5.7 | 8.0 | 5.3 | 7.6 | 4.84 | 56 | 22 |
| *P. australe* | MLP 84-III-9-12 | | | | 8.54 | 5.6 | 8.0 | 5.1 | 7.6 | 4.52 | 56.2 | 22.5 |
| *P. australe* | CORD-PZ 1387 | | | | 8.0 | 4.92 | 7.7 | 4.8 | 7.46 | 4.2 | | |
| *P. australe* | CORD-PZ 1287 | | | | 8.0 | 5.7 | 7.4 | 5.1 | 7.6 | 4.24 | | |
| *P. australe* | CORD-PZ 1379 | | | | 8.3 | 5.1 | 7.86 | 4.74 | 7.6 | 5.3 | | |
| *P. australe* | CORD-PZ 1381 | 6.44 | 4.6 | 4.9 | 8.7 | 5.4 | 8.8 | 5 | 7.22 | 4.18 | 56.3 | 23 |
| *P. australe* | CORD-PZ 1551 | 5.9 | 5.2 | 5.18 | 8.22 | 5.4 | 8.24 | 4.9 | 7.54 | 4.1 | 58.84 | 22.2 |
| *P. australe* | CORD-PZ 25 (# de campo) | 5.7 | 4.6 | 4.76 | 8.24 | 5.2 | 7.4 | 5.3 | 7.1 | 4.5 | 53.3 | 22.46 |
| *P. australe* | CORD-PZ 1209 | 7.1 | 5.34 | 5.2 | 8.0 | 5.1 | 7.6 | 4.9 | 7.36 | 3.94 | 54.9 | 21.6 |
| *P. australe* | CORD-PZ 1207 | | | | 9.2 | 5.54 | 8.0 | 5.1 | 7.54 | 4.24 | | |
| *P. australe* | CORD-PZ 1389 | | | | 8.55 | 5.55 | 7.6 | 5.0 | 7.2 | 4.28 | | |
| *P. australe* | CORD-1364 | | | | 8.0 | 5.1 | 7.3 | 5.0 | 6.8 | 3.96 | 53.3 | 20.7 |
| *P. australe* | YPM-PU 15598 | 6.9 | 5.28 | 5.03 | 8.3 | 5.34 | 7.12 | 4.72 | 6.98 | 3.88 | 54.12 | 22.14 |
| *P. australe* | YPM-PU 15643 | 6.68 | 5.5 | 5.3 | 8.24 | 5.22 | 7.87 | 4.7 | 7.0 | 3.9 | | |
| *P. australe* | YPM-PU 15189 | 6.75 | 5.04 | 5.4 | 8.6 | 5.42 | 8.1 | 5.14 | 7.1 | 4.08 | 54.9 | 24.8 |
| *P. australe* | YPM-PU 15828 | 6.06 | 5.28 | 5.28 | 9.6 | 5.72 | 8.22 | 5.5 | 8.2 | 4.53 | 59 | 24.24 |
| *P. praerutilum* | MACN-A 3989 | 3.7 | 3.5 | 3.5 | | | 6.0 | 4.0 | 6.1 | 3.3 | 44.2 | 18.6 |
| *P. praerutilum* | MACN-A 3990 | 4.5 | 4.2 | 4.3 | 7.0 | 4.6 | 6.8 | 4.2 | 6.0 | 2.9 | | |

| Taxon | Specimen No. | I1 md | I2 md | I3 md | M1 md | M1 ll | M2 md | M2 ll | M3 md | M3 ll | Pal. l | Pal. w |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *P. praerutilum* | MACN-A 1081 | 4.2 | 3.78 | 3.8 | | | | | 6.3 | 3.4 | 44.14 | 18.3 |
| *P. praerutilum* | MACN-A 3297 | 4.1 | 3.94 | 3.92 | 6.67 | 4.32 | 6.14 | 4.1 | 6.24 | 3.24 | | |
| *P. praerutilum* | MACN-A 1777 | | | | 6.86 | 4.56 | 6.5 | 4.12 | | | | |
| *P. praerutilum* | MACN-A 1778 | | | | 6.86 | 4.25 | 6.48 | 4 | 5.87 | 3.3 | | |
| *P. praerutilum* | MLP 12-1913 | | | | | | | | | | | |
| *P. praerutilum* | MLP 12-2090 | | | | | | 6.4 | 4.14 | 6.06 | 3.34 | | |
| *P. praerutilum* | MLP 74-II-1-2 | | | | 6.86 | 4.64 | | | | | | |
| *P. praerutilum* | MLP 12-1809 | | | | 7.4 | 4.3 | 6.7 | 3.8 | 5.56 | 3.12 | | |
| *P. praerutilum* | MLP 12-2709 | | | | 6.66 | 4.56 | 6.36 | 4.16 | | | | |
| *P. praerutilum* | MLP 12-2730 | | | | 6.34 | 4.38 | 6.08 | 4.3 | | | | |
| *P. praerutilum* | CORD-PZ 1197 | 3.8 | 3.5 | 3.7 | 6.34 | 4.1 | 6.1 | 3.9 | 5.5 | 3.1 | 42.36 | 18.63 |
| *P. praerutilum* | CORD-PZ 1208 | | | | 7 | 4.6 | 6.2 | 4.1 | 5.9 | 3.6 | | |
| *P. praerutilum* | CORD-PZ 1154 | | | | 7.3 | 4.6 | 6.8 | 4 | 6.8 | 3.3 | | |
| *P. praerutilum* | YPM-PU 15286 | | | | 6.88 | 4.14 | 5.58 | 3.8 | 6.34 | 3.3 | 45.5 | 19.8 |
| *P. praerutilum* (labeled *P. attenuatum*) | YPM-PU 15665 | | | | 6.44 | 4.6 | 6.15 | 4.08 | 5.67 | 3.36 | 44.2 | 18.7 |
| *P. praerutilum* (labeled *P. attenuatum*) | AMNH 9187 | | | | 6.62 | 4.0 | 5.86 | 3.65 | 5.9 | 3.01 | 43.45 | 18.67 |
| *P. praerutilum* ("anomalous") | MLP 26-IV-15-1 | 5.18 | 3.72 | | 6.5 | 4.1 | 6.0 | 3.6 | 5.7 | 3.14 | 45.2 | 19.1 |
| *P. praerutilum* ("anomalous") | MACN-A 9653 | 5.0 | 3.66 | 3.9 | 6.3 | 3.84 | 5.6 | 3.55 | 5.36 | 3.0 | 41.58 | 17.5 |
| *P. praerutilum* (LdL) | SGOPV 3835 | 4.1 | 3.74 | 3.7 | 6.3 | 3.8 | 5.62 | 3.6 | 5.54 | 3.14 | | |
| *P. praerutilum* (LdL) | SGOPV 3941 | 3.7 | 3.2 | 3.5 | 6.38 | 4.0 | 6.44 | 3.9 | | | | |
| *P. praerutilum* (LdL) | SGOPV 3826 | | | | 6.7 | 4.64 | 6.3 | 4.18 | 5.8 | 3.64 | | |
| *P. rectus* (*= P. praerutilum?*) | MACN-A 4005 | | | | 6.05 | 3.8 | 5.86 | 3.4 | 5.48 | 3.1 | | |
| *P. compressidens* | MACN-A 4029 | | | | 7.7 | 3.66 | 6.8 | 3.4 | | | | |
| *P. diastematum (=?)* | MACN-A 4044 | | | | 6.96 | 4.14 | 6.56 | 3.9 | 6.24 | 3.24 | | |
| *P. attenuatum* (type) | MACN-A 524 | | | | 6.5 | 4.1 | 5.6 | 3.6 | 5.4 | 3.0 | | |
| *P. attenuatum* | MLP 12-2706 | | | | 6.0 | 4.2 | 5.6 | 3.9 | | | | |
| *"P. globosum" (= P. attenuatum)* | MACN-A 4049 | | | | 6.36 | 4.80 | 6.0 | 4.22 | 6.0 | 3.40 | 42.0 | 20.7 |
| *"P. icochiloides" (=P. attenuatum)* | MACN-A 4021 | | | | 6.40 | 3.90 | | | | | | |
| *P. attenuatum* | CORD-PZ 1222 | 4.0 | 3.70 | 3.68 | 5.80 | 3.74 | | | | | | |

Chapter 3. New hegetotheriids (Typotheria, Notoungulata) from the Laguna del Laja region, and a phylogeny of Hegetotheriidae

LIST OF FIGURES AND TABLES

Chapter 3. New hegetotheriids (Typotheria, Notoungulata) from the Laguna del Laja region, and a phylogeny of Hegetotheriidae

## INTRODUCTION

Over the last 25 years, fossils collected from the Andes of Chile have provided a robust and insightful archive of mammal evolution in South America (Wyss *et al*., 1990, 1993, 1994; Flynn *et al*., 1995, 2002a, 2002b, 2003, 2008; Croft, 2001; Croft *et al*., 2003a, 2003b, 2004, 2007, 2008; Reguero *et al*., 2003; Hitz *et al*., 2000, 2006; Bostelmann *et al*., 2013). Miocene-aged fossils from near Laguna del Laja (LdL) (~37.5°S, 71°W), in the Andean Main Range of central Chile, contribute to this growing body of research (Wertheim, 2007; Flynn *et al*., 2008; Shockey *et al*., 2012; Luna, Ch. 2). Five field seasons in the LdL region (2001-2005) produced abundant, well-preserved fossils from five geographically distinct, but stratigraphically overlapping collecting areas southeast of the lake – informally termed Cerro Los Pinos, Estero Correntoso, Estero Campamento, Estero Trapa Trapa West, and Estero Trapa Trapa East (Herriot, 2006; Flynn *et al*., 2008) (figs. 3.1, 3.2). Strata in these well-mapped (1:20,000 scale) collecting areas include several interbedded tuffs, ignimbrites, and basalts, providing a robust stratigraphic and geochronologic framework for recovered fossils (figs. 3.1, 3.2) (Herriot, 2006; Flynn *et al*., 2008). Although fossils occur throughout ~2 km of stratigraphic section, spanning ~20-10 Ma in age, most specimens, and all the fossils discussed herein, were recovered from portions of the Cura-Mallín Formation (CMF) ranging between ~20-14 Ma in age (fig. 3.2) (Herriot, 2006; Flynn *et al*., 2008). The CMF in the Laguna del Laja region consists primarily of strongly folded, volcaniclastic strata, interpreted to have been deposited as

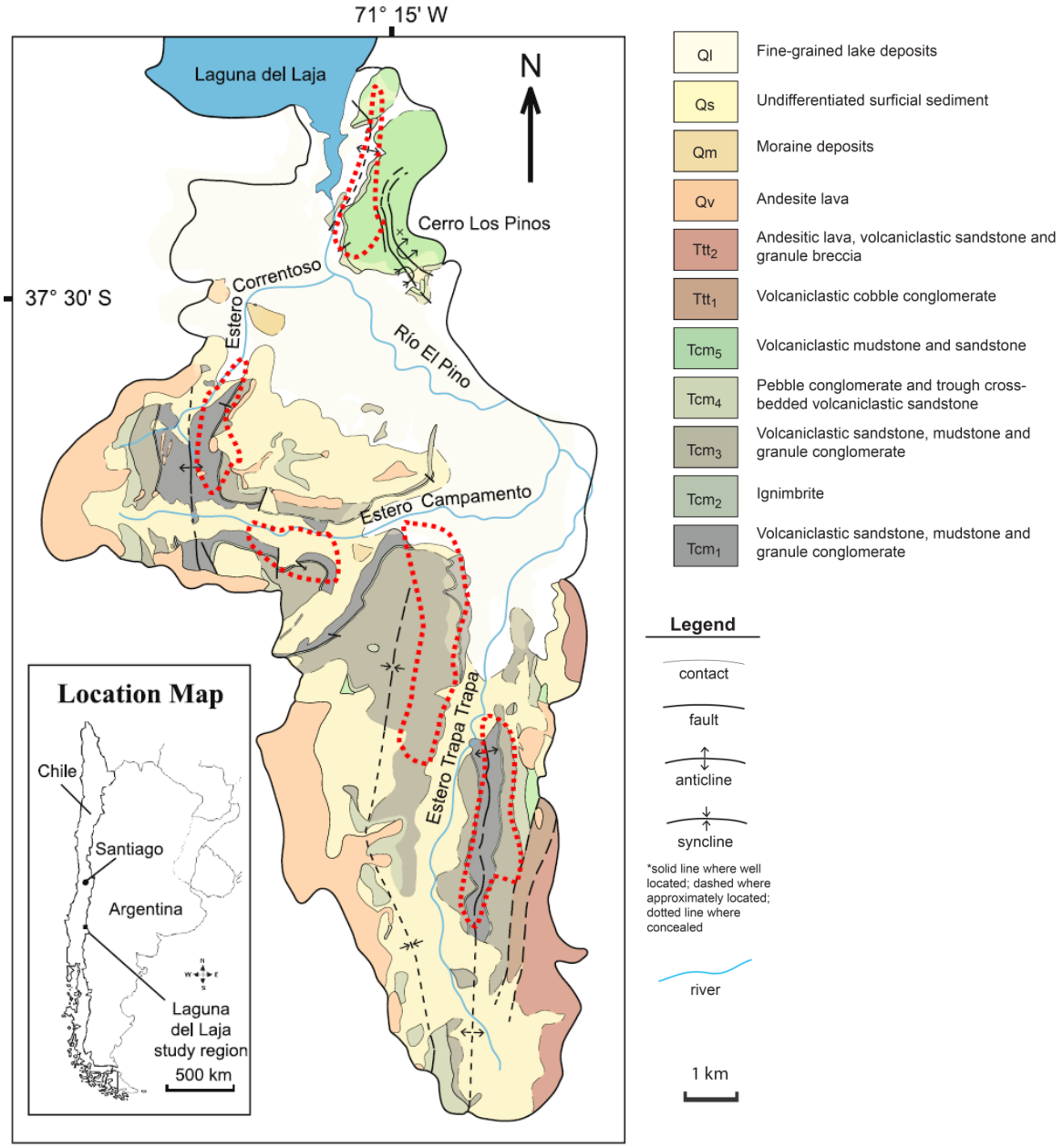


FIGURE 3.1. Map of the Laguna del Laja study area. Generalized geological map showing the sedmimentary units discussed in the text. Fossil mammal sampling subregions are encolosed by red, stippled lines. These collecting regions are infromally designated as (from north to south) Cerro Los Pinos, Estero Correntoso, Estero Campamento, Estero Trapa Trapa West, and Estero Trapa Trapa East. Inset shows the location of the study area within Chile. Modified from Flynn et al., 2008.

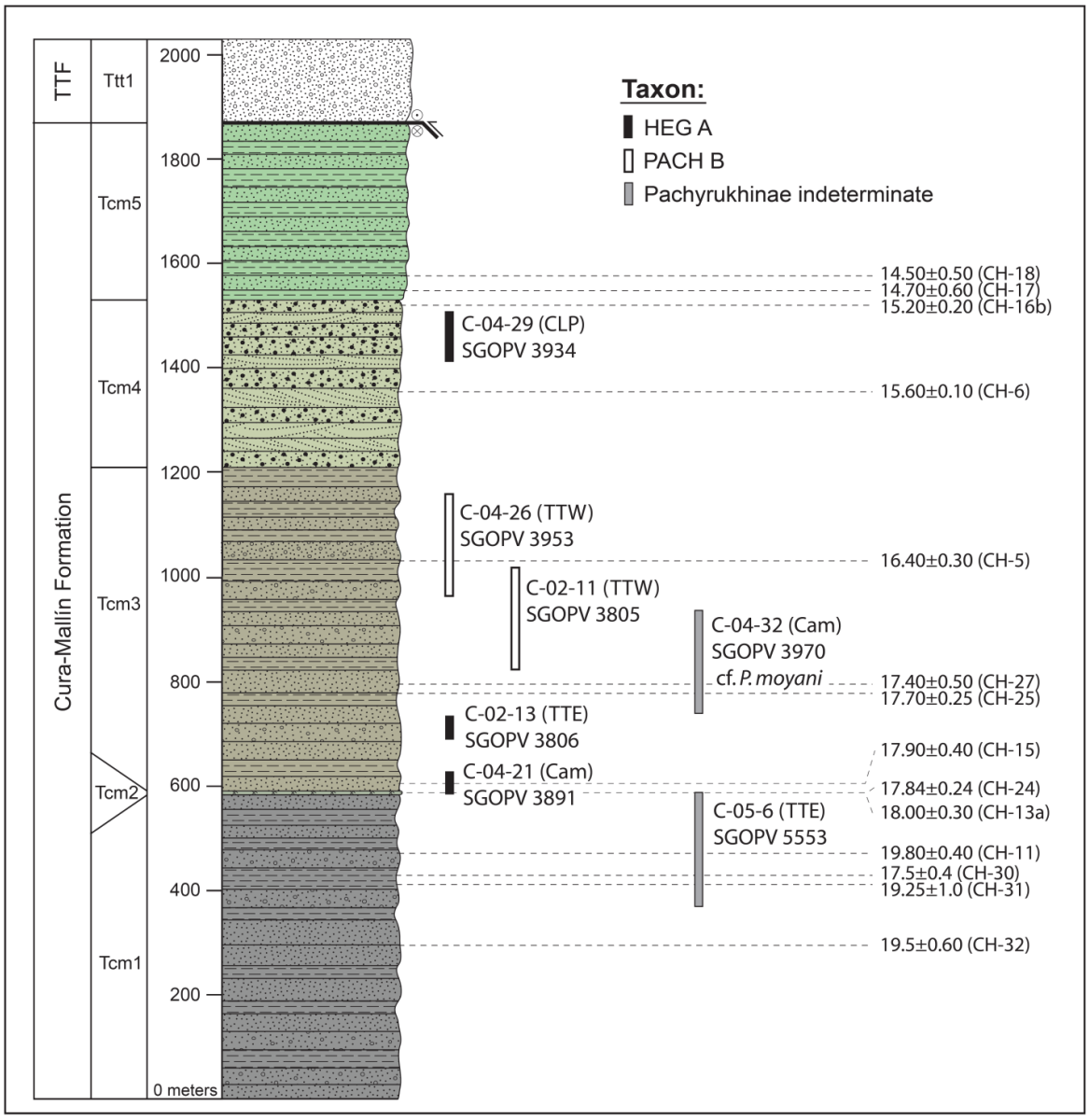


FIGURE 3.2. Composite stratigraphic section of the Cura-Mallín Formation exposed in the region southeast of Laguna del Laja. On the right, $^{40}Ar/^{39}Ar$ dates are indicated, with samples used for radioisotope analyses in parantheses. Stratigraphic positions of hegetotheriid specimens inlcude locality numbers (with collecting regions in parantheses; abbreviations listed below) and specimen numbers (SGOPV). The vertical height of bars associated with each specimen/locality represent the level uncertainty in stratigraphic position, with short bars indicating well-constrained stratigraphic positions and longer bars indicating moderately to poorly constrained stratigraphic positions. See fig. 1.6 for stratigraphic column legened. Abbreviations: Cam = Estero Campamento; CLP = Cerro Los Pinos; TTE = Estero Trapa Trapa East; TTW = Estero Trapa Trapa West.

lahars within an intra-montane basin (Herriott, 2006). To date, the majority of fossils described from the LdL region represent new taxa, including some 20 new species of rodents (Wertheim, 2007), three interatheriines (Ch. 2), and a leontiniid (Shockey *et al*., 2012). This study provides the first detailed report of hegetotheriids from the CMF southeast of LdL, adding two new species to this growing list of novel taxa from the LdL region.

Hegetotheriids are small-to-medium sized typotherian notoungulates, often considered broadly convergent with rodents or lagomorphs (Ameghino, 1889; Sinclair, 1909; Kraglievich, 1926; Simpson, 1945b; Elissamburu, 2004; Shockey and Anaya, 2008). Although Simpson (1945a; 1967) proposed that this group represents a separate order ("Hegetotheria"), distinct from Typotheria, all relevant phylogenetic analyses regard Hegetotheriidae as constituting a clade within Typotheria (Cifelli, 1993; Billet *et al*., 2009; Billet, 2010; Reguero and Prevosti, 2010; Kramarz and Paz, 2013), thus validating the concept of Hegetotheriidae as originally conceived by Ameghino (1894). Phylogenetic studies suggest close affinities between hegetotheriids, "archaeohyracids," and mesotheriids, but the precise relationships of these groups remains an open question (compare Cifelli, 1993; Croft *et al*. 2003a; Croft and Anaya, 2006; Billet *et al*., 2009; Billet, 2010; Reguero and Prevosti, 2010; Kramarz and Paz, 2013). Within Hegetotheriidae, two sub-groups are generally recognized, Hegetotheriinae and Pachyrukhinae (Simpson, 1945a; McKenna and Bell, 1997). Hegetotheriines are characterized by a complete dental series and long distal fusion of the tibia and fibula, whereas pachyrukhines are distinguished by the reduction or absence of I2-C/i3-c, absence of a sagittal crest, extremely large orbits, and large mastoid bullae that are easily visible in dorsal view of the skull. Support for pachyrukhine monophyly is robust and consistent (Cerdeño and Bond, 1998; Croft and Anaya, 2006; Billet *et al*., 2009; Reguero and Prevosti, 2010; Kramarz and Paz, 2013), but it is unclear whether

hegetotheriines are paraphyletic (Croft and Anaya, 2006; Reguero *et al*., 2007; Reguero and Prevosti, 2010) or monophyletic (Billet *et al*., 2009; Kramarz and Paz, 2013).

Hegetotheriids are certainly recognized by the Deseadan SALMA (late Oligocene), but their earliest record may extend into the Tinguiririan SALMA (early Oligocene) (Reguero, 1993, 1999; Flynn *et al*., 2003; Croft *et al*., 2008; Dozo *et al*., 2014). Hegetotheriid diversity is highest in the Deseadan, with two hegetotheriine genera (*Sallatherium*, *Prohegetotherium*) and three pachyrukhine genera (*Propachyrucos*, *Medistylus*, *Prosotherium*) recognized in this interval, primarily from Argentine Patagonia (Loomis, 1914; Simpson, 1945b; Reguero and Cerdeño, 2005; Reguero *et al*., 2007); Deseadan hegetotheriines are also known from Bolivia, Uruguay, and northern Argentina (Reguero and Cerdeño, 2005). The latest record of hegetotheriines is from the Huayquerian SALMA (late Miocene) (Cerdeño and Montalvo, 2002), while pachyrukhines persist into the Marplatan (late Pliocene-early Pleistocene) or possibly Ensenadan (early Pleistocene) SALMAs (Cerdeño and Reguero, 1998). In recent years, several hegetotheriids from Bolivia, Uruguay, and Argentina have been described or revised (Cerdeño and Reguero, 1998; Cerdeño and Montalvo, 2002; Reguero and Cerdeño, 2005; Croft and Anaya, 2006; Reguero *et al*., 2007; Kramaz and Paz, 2013). Although hegetotheriids have been previously reported from the late early Miocene (and possibly Oligocene) of Chile (Flynn *et al*., 2002a, 2002b; Croft *et al*., 2004, 2008), the fossils described herein, all recovered from exposures of the CMF southeast of LdL, represent the first novel hegetotheriids from Chile.

## MATERIALS, ABBREVIATIONS, AND METHODS

MATERIALS. The primary impetus for this study was the recent recovery (2001-2005) of several hundred fossil mammal specimens from the Laguna del Laja region, of which the hegetotheriids are described herein. These specimens will be accessioned in the fossil vertebrate collection of the Museo Nacional de Historia Natural, Santiago, Chile (SGOPV). Other specimens and publications from which data were obtained are discussed in the text and/or listed in appendix 3.1.

ABBREVIATIONS. The following institutions (with corresponding abbreviations used throughout this text) provided access to specimens examined in this study: American Museum of Natural History, New York (AMNH); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina (MACN; MACN-A refers to specimens that belong to the Ameghino collection); Museo de La Plata, La Plata, Argentina (MLP); Yale Peabody Museum, Princeton University Collection, New Haven (YPM-PU).

The following abbreviations apply to dental descriptions: I/i for upper and lower incisors, C/c for upper and lower canines, P/p for upper and lower premolars, and M/m for upper and lower molars. Descriptions of dental morphology follow the nomenclature of Reguero (1999). Dental orientation is indicated by four cardinal directions: mesial, distal, lingual, and labial (following Smith and Dodson, 2003). Measurements were obtained with KÖLN calipers. Mesiodistal dimensions (lengths) of teeth were obtained at the greatest length of the ectoloph; labiolingual dimensions (transverse widths) of cheek teeth represent maximum widths between the ecto- and entolophs, perpendicular to the mesiodistal axis of the teeth. A recent illustration of these tooth measurements is provided by Billet *et al*. (2009; fig. 1 therein).

METHODS. Our cladistic analysis of hegetotheriids incorporates 17 taxa, including the two described in the present study, and a various taxa assessed phylogenetically by Cerdeño and Bond (1998), Croft and Anaya (2006), Billet *et al*. (2009), Reguero and Prevosti (2010), and Kramarz and Paz (2013). In accordance with the recent results of Billet *et al*. (2009) and Kramarz and Paz (2013), a clade of "late archaeohyracids" (*Archaeotypotherium*, (*Protarchaeohyrax*, *Archaeohyrax*)) was selected as the outgroup to Hegetotheriidae. Outgroup character states were determined by reconstructing the ancestral character states of this clade, using the phylogenetic results of Billet *et al*. (2009), and by directly consulting specimens and/or descriptions of these taxa (see appendix 3.1). Taxa were coded for 36 characters (Appendices 3.2 and 3.3). Most characters examined were obtained from published studies (Croft *et al*., 2006; Billet *et al*., 2009; Kramarz and Paz, 2013), but several character descriptions and codings were revised to increase clarity or to incorporate new observations. Appendix 3.2 includes a detailed list discussing similarities and departures from character descriptions of previous studies.

A parsimony analysis was performed with "Tree analysis using New Technology" (TNT) v1.1 (Goloboff *et al*., 2003, 2008). Given the high degree of homoplasy observed in previous studies (Cifelli, 1993; Billet *et al*., 2009; Kramarz and Paz, 2013), character weights were determined using implied weighting (k=3), which estimates the reliability of characters during tree search (Goloboff, 1993); all characters were treated as unordered. A "New technology search" using Sectorial Search and Tree Fusing (Goloboff, 1999, Goloboff *et al*., 2008) yielded two equally parsimonious trees. Support for each node of the consensus tree was determined with TNT (Goloboff *et al*., 2008) Symmetric Resampling (P=33) (Goloboff *et al*., 2003), using 500 replicates with Tree Bisection Reconnection (TBR) as the swapping algorithm (Goloboff and Farris, 2001).

Isotopic ages of tuffs, ignimbrites, and lava flows from the LdL region are reported by Herriot (2006) and Flynn *et al*. (2008); the methods and results of these analyses will be more fully documented by Gans *et al*. (in progress).

## SYSTEMATIC PALEONTOLOGY

## NOTOUNGULATA ROTH, 1903

## TYPOTHERIA ZITTEL, 1893

## HEGETOTHERIIDAE AMEGHINO, 1894

### Hegetotheriidae gen. *et* sp. *nov.* A

Fig. 3.3, Table 3.1

SYNONYMY: "?*Hegetotherium*," Flynn *et al*., 2008: table 1.

"Hegetotheriidae, unidnet.," Flynn *et al*., 2008: table 1.

"Typotheria, unidnet.," Flynn *et al*., 2008: table 1.

HOLOTYPE: SGOPV 3806 consists of a partial rostrum bearing a nearly complete left dentition (complete C-M3, partial I2-3). At least portions of the right dentition remain encased in matrix.

REFERRED MATERIAL: SGOPV 3891, right ?M1 (or possibly M2), lower right ?premolar, and fragmentary right m3, found isolated but close together; SGOPV 3934, right m2-3 and ?p4 (although no trace of the mandibular ramus is preserved, these teeth are evidently preserved in life position).

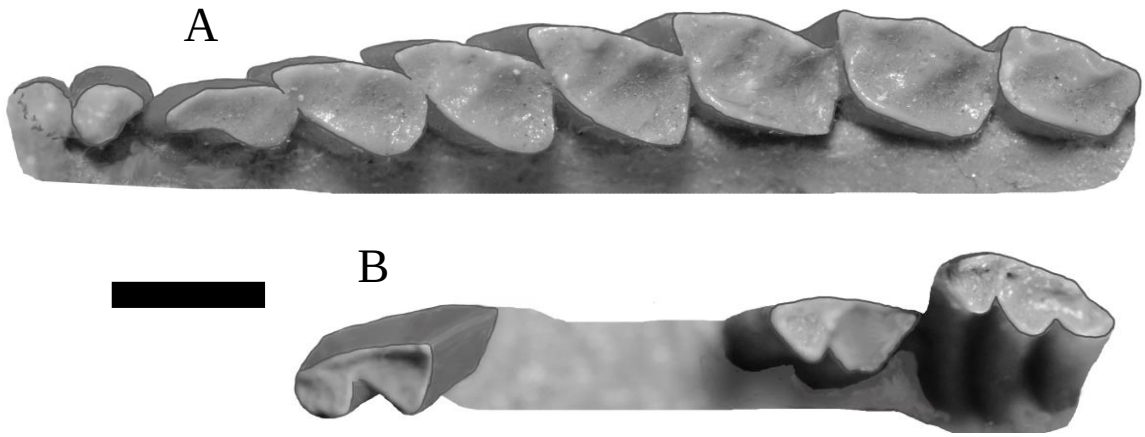


FIGURE 3.3. Dentitions of Hegetotheriidae gen. *et* sp. *nov*. A. **A**: Holotype SGOPV 3806, left I3-M3 in occlusal view (I3 partially embedded in matrix; I2 also preserved, but almost completely embedded in matrix and not illustrated). **B**: SGOPV 3934, right m2-3 and ?p4 (shown as left). These two specimens were not found in association; see text for further discussion. Sclae bar = 0.5 cm.

**TABLE 3.1: Dental measurements (mm) for lower dentition of HEG A.**
md = mesiodistal; ll = labiolingual

| Tooth | SGOPV 3806 | SGOPV 3891 | SGOPV 3934 |
|---|---|---|---|
| p4 md | | 4.92† | 5.18† |
| p4 ll | | 2.59† | 2.62† |
| m2 md | | | 4.91 |
| m2 ll | | | 2.79 |
| m3 md | | 6.3*† | 6.24 |
| m3 ll | | 2.3*† | 2.24 |
| C md | 2.53 | | |
| Cll | 1.91 | | |
| P1 md | 4.39 | | |
| P1 ll | 2.12 | | |
| P2md | 5.13 | | |
| P2 ll | 2.64 | | |
| P3 md | 5.32 | | |
| P3 ll | 3.18 | | |
| P4 md | 5.41 | | |
| P4 ll | 3.24 | | |
| M1 md | 5.64 | 5.22† | |
| M1 ll | 3.35 | 3.06† | |
| M2 md | 5.92 | | |
| M2 ll | 3.34 | | |
| M3 md | 4.93 | | |
| M3 ll | 2.79 | | |

*measurement approximate
† tooth position uncertain

DISTRIBUTION AND AGE: Specimens were collected from three localities southeast of Laguna del Laja. The holotype (SGOPV 3806) was recovered from Estero Trapa Trapa East (site C-02-13) within unit $Tcm_3$ of the Cura-Mallín Formation (Herriott, 2006) (figs. 3.1, 3.2). Site C-02-13 lies about 75 m stratigraphically below an ash fall tuff (CH-25) which has yielded an $^{40}Ar/^{39}Ar$ age of 17.70 ± 0.25 Ma, and about 100 m above an ignimbrite (CH-15) dated to 17.90 ± 0.40 Ma (Herriot, 2006; Flynn *et al*., 2008) (fig. 3.2). These bracketing horizons indicate an age of ~17.8 Ma for the holotype. SGOPV 3891 was recovered from Estero Campamento (site C-04-21), also from within unit $Tcm_3$ of the CMF, approximately 10 meters above a thick ignimbrite (unit $Tcm_2$); two samples from this ignimbrite yielded ages of 17.84 ± 0.24 Ma (CH-24) and 18.00 ± 0.30 Ma (CH-13a) (figs. 3.1, 3.2). SGOPV 3934 was collected at Cerro Los Pinos (site C-04-29), from unit $Tcm_4$ of the CMF; although the stratigraphic position of this locality is known with limited precision, it is bracketed by horizons dated to 15.20 ± 0.20 Ma (CH-CH-16b) and 15.60 ± 0.10 Ma (CH-6) (figs. 3.1, 3.2). In sum, the stratigraphic positions of these three specimens indicate an age range of ~15.2-18 Ma for the occurrence of this taxon at LdL.

DIAGNOSIS: The diagnosis of Hegetotheriidae gen. *et* sp. *nov*. A (informally referred to herein as HEG A) is based primarily on the more completely known upper dentition (fig. 3.1). In possessing a complete and unreduced upper dental series (I1 was undoubtedly present but is not preserved), HEG A differs from pachyrukhines, wherein I2-C are highly reduced or lost (P1 is also lost in later diverging forms; see figs. 3.8 and 3.9 for phylogenetic conclusions). The lingual walls of the upper molars of HEG A are continuous and straight, lacking any trace of the salient lingual sulcus that characterizes the "bi-lobed" upper molars of *Propachyrukhos*, *Medistylus*, *Prosotherium*, and *Hegetotheriopsis*. In HEG A the labial and posterior walls of M1 form a right angle (character 10, state 1), an advanced condition

compared to *Hegetotheriopsis* and *Sallatherium* (the earliest-diverging hegetotheriids in our phylogeny), where this angle is obtuse. HEG A is also significantly smaller than *Sallatherium*, has a more robust upper canine, and the lingual faces of P4-M3 are straight, resulting in rectangular outlines (in *Sallatherium* the lingual faces of these teeth are curved, producing ovoid outlines).

Although various characters observed in HEG A occur in differing combinations in other well-known "hegetotheriines," the constellation of features seen in HEG A is unique. HEG A is similar to *Hegetotherium* in having roughly rectangular molars in outline. On the other hand, HEG A is smaller than *Hegetotherium*, its P2/3 are subequal in size (in *Hegetotherium*, P2 is notably smaller than P3), and M3 lacks the lingual sulcus that is often (but variably) present in *Hegetotherium*. HEG A falls within the size range reported for *Prohegetotherium schiaffinoi*, and P2 in both taxa is large (comparable in size to P3). In HEG A, however, M3 is quadrangular (in *P. schiaffinoi* the lingual face of M3 is more convex), I2/3 are separated by a diastema (*P. schiaffinoi* has a closed dental series), P3-4 lack the deep parastylar grooves seen in *P. schiaffinoi*, and the size difference between the premolars and molars is less marked than in *P. schiaffinoi*. In HEG A and *Prohegeotherium sculptum* the upper canine is positioned labially with respect to P1. These taxa differ, however, in that HEG A is smaller, its P2/3 are subequal in size (in *P. sculptum*, P2 is significantly narrower labiolingually than is P3), and its premolars lack the distinct parastyle groove exhibited by *P. sculptum* (note that *P. scultpum* is known from very fragmentary material).

In the phylogenetic analysis presented below (fig. 3.8), HEG A and *Hemihegetotherium* form a clade united by a single synapomorphy: the root of the upper canine lies labial to P1 (character 5, state 1). *Hemihegetotherium trilobus* and HEG A also

share a deep labial sulcus dividing the m3 talonid (character 18, state 2; see further discussion of this character in Remarks below). Nevertheless, HEG A is easily distinguished from *Hemihegetotherium* in that the former is significantly smaller, its P4-M3 are rectangular in outline (P4-M3 of *Hemihegetotherium* are convex lingually and ovoid in outline), and has a diastema between I2/3 (the dental series in *Hemihegetotherium* is closed).

HEG A is also diagnosed by a uniquely large P1, which is almost as long mesiodistally as the relatively large P2. In some specimens of *Sallatherium* and *Hegetotherium* P1 approaches the length of P2, but in these two taxa both teeth are significantly reduced compared to the posterior premolars and molars, whereas in HEG A P1 is only slightly smaller than the posterior premolars and molars (see fig. 3.4). In other "hegetotheriines" P1 is significantly smaller (especially mesiodistally) than P2-4, and is somewhat columnar in shape. In contrast, P1 of HEG A is long (fig. 3.4) and somewhat pear-shaped – broader posteriorly than anteriorly. This condition is most closely approximated by *Prohegetohterium sculptum*, where the anterior extension of P1 is nevertheless much smaller than in HEG A.

DESCRIPTION: HEG A (fig. 3.3) is a diminutive "hegetotheriine," comparable in tooth dimensions to *Prohegetotherium schiaffinoi*.

I1 is not preserved, and only the labial surfaces of I2/3 are exposed. Based on these partial remains, I2/3 are likely columnar in shape, and certainly separated by a diastema. The canine, also columnar, is significantly shorter mesiodistally than P1 (but still robust compared to the canine of *Sallatherium*, for example), and is positioned labially with respect to P1 (as in *Hemihegetotherium* and *Prohegetotherium sculptum*). P1 is significantly longer than the canine mesiodistally, but similar in labiolingual width; it is somewhat pear-shaped in occlusal outline (narrow anteriorly and broader posteriorly – the anterior and posterior

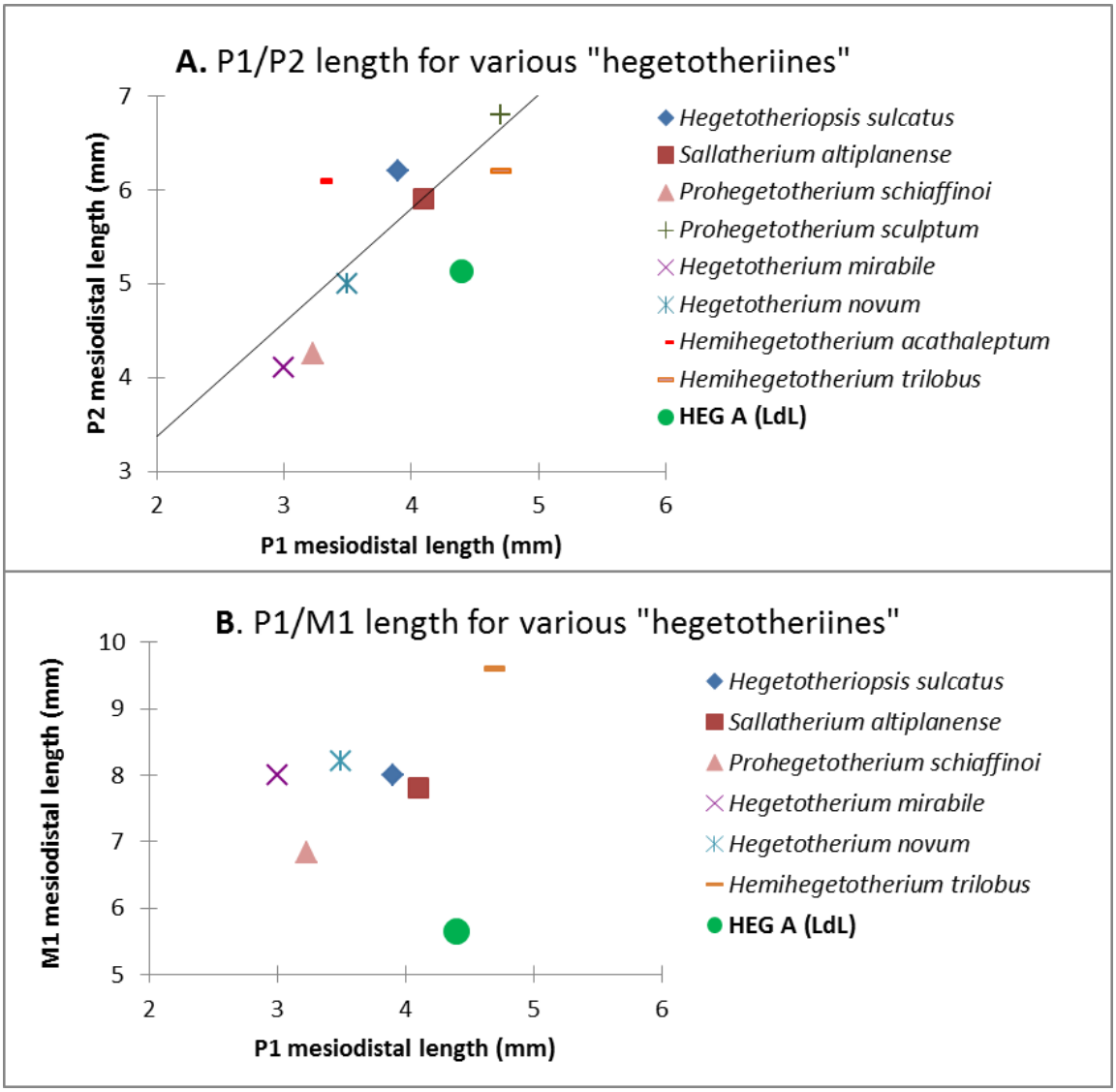


FIGURE 3.4. P1 mesiodistal length compared to P2 length (**A**) and M1 length (**B**) for various "hegetotheriines." **A**: A regression line is fit to the plot of P1/P2 lengths for all "hegetotheriines" except HEG A, to highlight that in HEG A P1 is atypically large relative to P2. **B**: *Prohegetotherium schiaffinoi* excluded because M1 length is unknown; *Hemihegeotherium achathaleptum* (P1 length 3.3; P2 length 11.4) excluded because M1 length exceeds the dimensions of the plot. Type specimens were used for measurements if available, otherwise measurements are taken from the literature. For each taxon, specimens used for measurements and pertinent publications are listed:
*Hegetotheriopsis sulcatus*: MACN Pv CH2015 (holotype); Kramarz *et al.*, 2013.
*Sallatherium altiplanense*: UF 91621 (holotype); Reguero and Cerdeño, 2005.
*Prohegetotherium schiaffinoi*: plotted measurements are averages from the following specimens:UF 91350, UF 91311, UF 91661, UF 91662, UF 172445, UF 172483; Reguero and Cerdeño, 2005.
*Prohegetotherium sculptum*: MACN-A 52-443.
*Hegetotherium mirabile*: YPM-PU 15542; Sinclair, 1909.
*Hegetotherium novum*: MACN 11749 (holotype); Bordas, 1939.
*Hemihegetotherium acathaleptum*: GUNLPam 151; Cerdeño and Montalvo, 2002.
*Hemihegetotherium trilobus*: plotted measurements are averages from the following specimens: MNHN-BOL-V 003669, MNHN-BOL-V 006604, MNHN-BOL-V 008628.
HEG A: SGOPV 3806 (holotype).

"lobes" being separated by a shallow vertical groove on the labial surface and deeper vertical groove on the lingual surface). P2-3 are slightly longer mesiodistally than P1, but significantly broader labiolingually. Although P2-3 are similar in size, P3 is slightly broader labiolingually. Both teeth are somewhat triangular in outline, having relatively straight labial and posterior margins, and smoothly concave lingual margins. P4-M2 are similar in size and shape; they are roughly rectangular in occlusal outline, with relatively straight labial, posterior, and lingual margins meeting nearly at right angles, and a slanting anterior margin that forms an obtuse angle against the lingual margin and acute angle against the labial margin (this "slant" diminishes posteriorly from P4-M2, the anterior margin becoming increasingly transverse). M3, smaller than P4-M2, is almost perfectly rectangular, having a transverse anterior margin (not "slanted" as in P4-M2). Although the labial surfaces of P2-M3 are quite flat, a very faint trace of a vertical paracone bulge occurs on P4-M2, and M2 bears an additional faint ridge between the para and metacones.

SGOPV 3891 and 3934 preserve lower premolars and molars. Although the precise identities of some of these teeth are uncertain, at least one tooth is likely p4. This tooth is bilobed, consisting of a roughly triangular trigonid (although the anterior "corner" of this triangle is rounded) and a triangular talonid separated by a deep sulcus labially, but having a flat wall lingually. The m2 and ?p4 are similar in size and morphology, except that the m2 trigonid is more triangular and its anterior margin is more pointed (rather than rounded as in ?p4). The m3 is mesiodistally longer than m2, having a small, triangular trigonid and a long talonid divided by a deep labial sulcus, giving m3 a "trilobed" appearance (as in *Hemihegetotherium trilobus*). The anterior lobe of the talonid comes to a rounded point labially, while the posterior lobe of the talonid is evenly curved. The lingual margin of m3 is smooth and flat. In SGOPV 3934, ?p4 and m2-3 may be preserved in series, but the ?p4 and

m2 occlusal surfaces sit far below that of m3 (~10 mm of the m3 crown height is exposed, compared to ~5 mm for ?p4 and m2), and the?p4 is strongly tilted anteriorly with respect to m2-3, indicating some post-mortem displacement. Over 10 mm of crown height is exposed for several teeth (?p4 and ?M1 of SGOPV 3891 and m3 of SGOPV 3934); these tall crowns do not taper towards the roots, clearly indicating hypselodonty. Upper and lower cheekteeth are curved vertically, the lowers being concave labially and the uppers concave lingually.

REMARKS: We are confident in referring the lower dentition of SGOPV 3891 and 3934 to HEG A, but emphasize that evidence for this action is somewhat circumstantial. SGOPV 3891 includes three isolated teeth (right ?M1, m3, and lower ?premolar) all found in extremely close proximity. The upper molar is essentially identical to the M1 of SGOPV 3806, and the size and morphology of the lower teeth fit expectations for the lower dentition of a relatively small "hegetotheriine" like HEG A. The two lower cheek teeth of SGOPV 3891 are also essentially identical to two of the three teeth in SGOPV 3934 (?p4 and m3). With these suggested associations, all "hegetotheriine" specimens thus far obtained from the LdL region are assigned to HEG A.

Although the lower teeth provided by SGOPV 3891 and 3934 reveal little diagnostic morphology, one feature merits note. In both specimens m3 bears a deep labial sulcus along the talonid, giving this tooth a trilobed shape. Although this morphology is typical of pachyrukhines, among "hegetotheriines" a trilobed m3 is only shared by *Hemihegetotherium trilobus* (*Hegetotherium mirabile* and *Hegetotheriopsis* have shallower lingual grooves on the m3 talonid). A trilobed m3 (character 18, state 2) is incorporated in our phylogenetic analysis. Hence, our phylogenetic results are influenced by the referral of SGOPV 3891 and 3934 to HEG A (proposed above). Scoring HEG A as having a trilobed m3 results in this character mapping as a synapomorphy uniting HEG A, *Hegetotherium*, and Pachyrukhinae

(with a secondary loss in some species of *Hemihegetotherium*). Should future findings suggest that our proposed associations of upper and lower teeth of HEG A are invalid, preliminary analyses suggest that our phylogenetic results would be influenced only slightly. That is, if we do not code HEG A for a trilobed m3 (leaving character 18 unknown) the overall topology of the resulting tree is extremely similar to the tree presented in figs. 3.8 and 3.9. In fact, the association between HEG A, *Hegetotherium*, and Pachyrukhinae remains supported, and the only differences between the trees are the positions of *Prohegetotherium* and *Hegetotherium*. This alternate phylogeny can be summarized as: (*Hegetotheriopsis*, (*Sallatherium*, (*Prohegetotherium sculptum*, (*P. schiaffinoi*, (*Hegetotherium*, ((HEG A, *Hemihegetotherium*), Pachyrukhinae))))))).

Pachyrukhinae gen. *et* sp. *nov*. B

Fig. 3.5, Table 3.2

SYNONYMY: *Paedotherium minor*, Flynn *et al*., 2008: 414, table 1; 417, fig. 4g.

HOLOTYPE: SGOPV 3805 consists of a partial palate with a complete upper right dentition (I1, P2-M3), as well as fragmentary left I1 and P2-M1.

REFERRED MATERIAL: SGOPV 3953, partial palate bearing left I1 and fragmentary left P2-M2.

DISTRIBUTION AND AGE: Both specimens were recovered from the Estero Trapa Trapa West collecting region, southeast of Laguna del Laja, in the Andes of central Chile (figs. 3.1, 3.2). The holotype SGOPV 3805 was recovered from locality C-02-11 within unit $Tcm_3$ of the Cura-Mallín Formation (Herriott, 2006) (figs. 3.1, 3.2). Although the

stratigraphic position of this locality is known only to within ~200 m, it is bracketed by horizons that have yielded $^{40}Ar/^{39}Ar$ ages of 16.4 ± 0.30 Ma (ignimbrite CH-27) and 17.40 ± 0.50 Ma (ash-fall tuff CH-27) (Herriot, 2006; Flynn *et al*., 2008) (fig. 3.2). SGOPV 3953 was recovered from locality C-04-26, also within unit $Tcm_3$ of the CMF (Herriott, 2006) (fig. 3.1, 3.2). The stratigraphic position of C-04-26 is known only to within ~200 m, but this locality is bracketed by horizons dated to 15.60 ± 0.10 Ma (ignimbrite CH-6) and 17.40 ± 0.50 Ma (ash-fall tuff CH-27). (Herriot, 2006; Flynn *et al*., 2008) (fig. 3.2). In sum, the stratigraphic provenance of these two specimens indicates an age range of ~15.6-17.4 Ma for this taxon at LdL.

DIAGNOSIS: The diagnosis of Pachyrukhinae gen. et sp. nov. B (informally referred to below as PACH B) is necessarily limited to the upper dentition (fig. 3.5). The close affinities of PACH B with *Pachyrukhos, Paedotherium,* and *Tremacyllus* are indicated by upper molars with planar lingual faces (a salient lingual sulcus occurs in *Propachyrucos*, *Medistylus*, and *Prosotherium*) and the lack of any trace of I2-P1. PACH B is especially similar in upper dental features to *Pachyrukhos*, but P3-4 are distinctly wider (labiolingually) and more triangular in occlusal outline (in *Pachyrukhos* they are roughly trapezoidal and relatively narrow; see fig. 3.6b-c) and P4-M2 bear salient labial ridges separated by distinct grooves (some specimens of *Pachyrukhos* bear subtle labial grooves on the cheek teeth, but the ridges and grooves of HEG B are much more pronounced). (Note: dental measurements [table 3.3, fig. 3.6] also indicates that, compared to *Pachyrukhos*, PACH B also has a relatively wider M1 [fig. 3.6d], an atypically small M3 [figs. 3.6f, 3.7], and P3-4 and M2 mesiodistal lengths that are near or below the lower size range of *Pachyrukhos* (figs. 3.6 b-c, 3.6e), but these differences are very subtle and of limited diagnostic value.) Compared to *Tremacyllus*, PACH B is distinguished by its larger size, M3 that is notably reduced in size


FIGURE 3.5. Holotype of of Pachyrukhinae gen. *et* sp. *nov*. B, SGOPV 3805, right I1-M3 (and partial left I1). **A**: Occlusal view; **B:** Labial view. Sclae bars = 0.5 cm.

**TABLE 3.2: Dental measurements (mm) for upper dentition of PACH B.**
md = mesiodistal; ll = labiolingual

| Tooth | SGOPV 3805 | SGOPV 3953 |
|---|---|---|
| I1 md | 8.04 | 8.25 |
| I1 ll | 1.27 | 1.34 |
| P2 md | 3.51 | 3.41 |
| P2 ll | 2.18 | |
| P3 md | 3.54 | 3.5* |
| P3 ll | 2.94 | 2.8* |
| P4 md | 3.76 | 3.9* |
| P4 ll | 3.06 | 3.2* |
| M1 md | 4.98 | 5.04 |
| M1 ll | 3.21 | 3.3* |
| M2 md | 4.42 | |
| M2 ll | 3.01 | |
| M3 md | 4.03 | |
| M3 ll | 2.34 | |

*measurement approximate

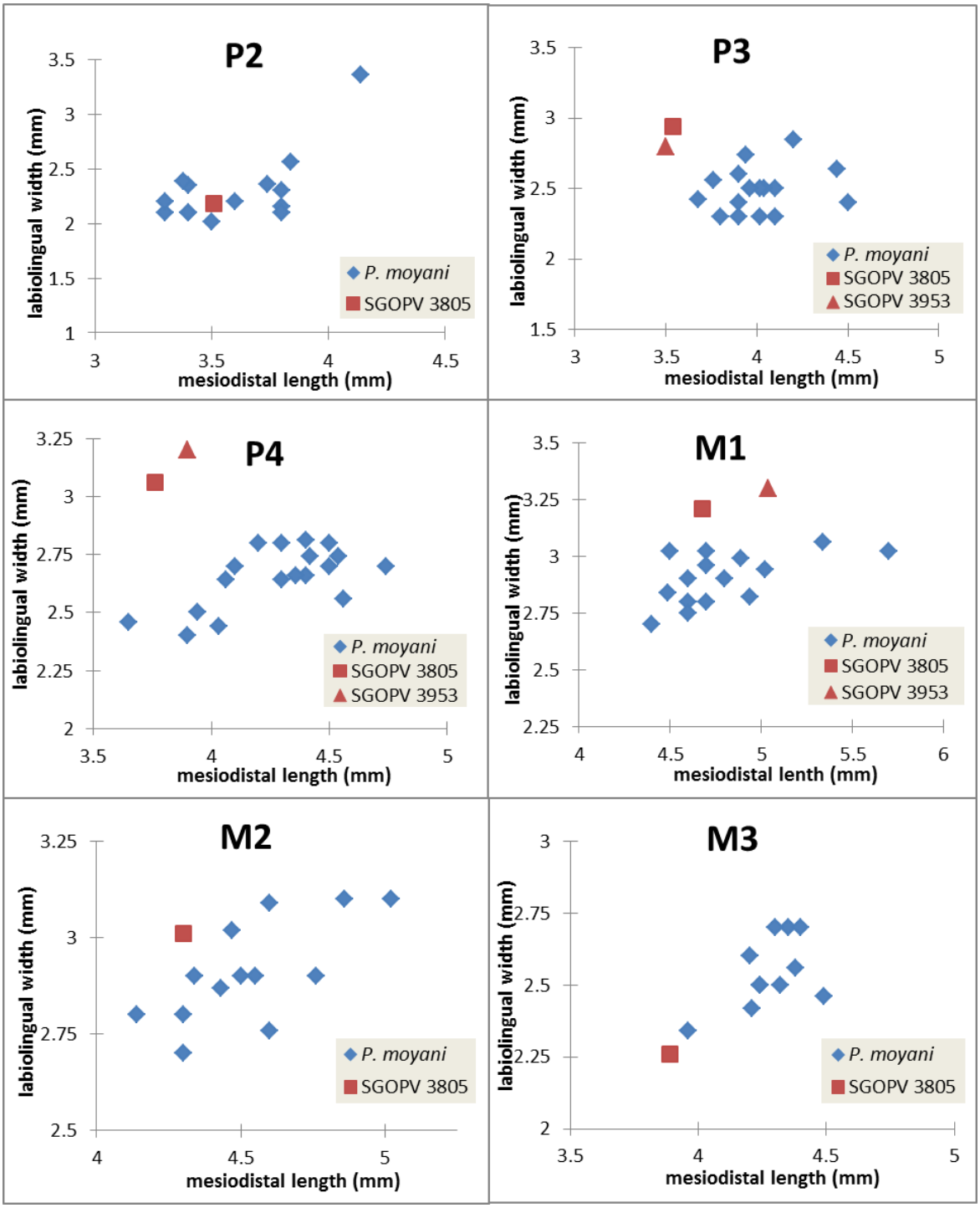


FIGURE 3.6. Length/width measurements of PACH B (SGOPV 3805, SGOPV 3953) and *Pachyrukhos moyani* cheek teeth. Most measurements for SGOPV 3952 are approximate. See table 3 for more detailed specimen information and measurements.

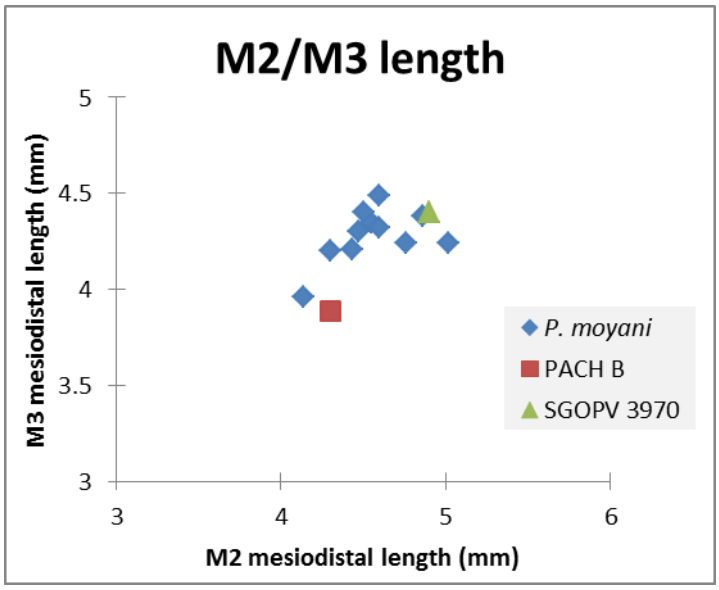


FIGURE 3.7. M1/M2 lengths of *P. moyani*, PACH B (SGOPV 3805), and SGOPV 3970 (cf. *P. moyani*). See table 3 for more detailed specimen information and measurements.

**TABLE 3.3: Measurements of cheek teeth in *Pachyruchos moyani*, PACH B, and LdL Pachyrukhinae indeterminate.**
md = mesiodistal; ll = labiolingual

| specimen number | P2 md | P2 ll | P3 md | P3 ll | P4 md | P4 ll | M1 md | M1 ll | M2 md | M2 ll | M3 md | M3 ll |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pachyrukhos moyani* | | | | | | | | | | | | |
| MACN-A 279 (holotype) | 3.8 | 2.3 | 4.2 | 2.85 | 4.5 | 2.7 | 4.7 | 3.02 | 4.55 | 2.9 | 4.35 | 2.7 |
| MACN-A 276 | 3.4 | 2.1 | 4.1 | 2.3 | 4.4 | 2.66 | 4.6 | 2.8 | 4.3 | 2.7 | 4.2 | 2.6 |
| MACN-A 319 | 3.5 | 2.02 | 3.8 | 2.3 | 3.9 | 2.4 | | | | | | |
| MACN-A 320 | 3.3 | 2.1 | 3.9 | 2.6 | 4.3 | 2.8 | 4.6 | 2.75 | 4.3 | 2.8 | | |
| MACN-A 321 | 3.4 | 2.35 | 4.1 | 2.5 | 4.2 | 2.8 | 4.5 | 3.02 | | | | |
| MLP 12-1986 | 3.8 | 2.16 | 4.04 | 2.5 | 4.56 | 2.56 | | | | | | |
| MLP 12-1989 | | | 4.02 | 2.3 | 3.94 | 2.5 | 4.8 | 2.9 | | | | |
| MLP 12-1998 | | | | | 4.06 | 2.64 | 4.4 | 2.7 | 5.02 | 3.1 | 4.24 | 2.5 |
| MLP 12-2018 | | | 3.9 | 2.4 | 3.65 | 2.46 | | | | | | |
| MLP 12-2075 | 3.6 | 2.2 | 3.76 | 2.56 | 4.1 | 2.7 | 4.7 | 2.8 | 4.5 | 2.9 | 4.4 | 2.7 |
| MLP 12-2086 | 3.4 | 2.1 | 4.02 | 2.5 | 4.3 | 2.64 | 4.7 | 2.96 | 4.14 | 2.8 | 3.96 | 2.34 |
| MLP 12-2087 | 3.3 | 2.2 | 3.9 | 2.3 | 4.5 | 2.8 | 4.6 | 2.9 | 4.34 | 2.9 | | |
| YPM-PU 14743 | 4.14 | 3.36 | 4.5 | 2.4 | 4.74 | 2.7 | 5.7 | 3.02 | 4.86 | 3.1 | 4.38 | 2.56 |
| YPM-PU 15369 | 3.8 | 2.1 | 3.96 | 2.5 | 4.36 | 2.66 | 4.49 | 2.84 | 4.6 | 2.76 | 4.32 | 2.5 |
| YPM-PU 15438 | 3.84 | 2.56 | 4.44 | 2.64 | 4.54 | 2.74 | 5.34 | 3.06 | 4.47 | 3.02 | 4.3 | 2.7 |
| YPM-PU 15603 | 3.74 | 2.36 | 3.94 | 2.74 | 4.42 | 2.74 | 5.02 | 2.94 | 4.76 | 2.9 | 4.24 | 2.5 |
| AMNH 9528 | 3.38 | 2.39 | 3.68 | 2.42 | 4.03 | 2.44 | 4.94 | 2.82 | 4.43 | 2.87 | 4.21 | 2.42 |
| AMNH 9558 | | | | | 4.4 | 2.81 | 4.89 | 2.99 | 4.6 | 3.09 | 4.49 | 2.46 |
| PACH B | | | | | | | | | | | | |
| SGOPV 3805 | 3.51 | 2.18 | 3.54 | 2.94 | 3.76 | 3.06 | 4.68 | 3.21 | 4.3 | 3.01 | 3.89 | 2.26 |
| SGOPV 3953 | 3.41 | | 3.5* | 2.8* | 3.9* | 3.2* | 5.04 | 3.3* | | | | |
| Pachyrukhinae *incertae sedis* | | | | | | | | | | | | |
| SGOPV 3970 (cf. P moyani) | | | | | | | | | 4.9* | | 4.4* | |
| SGOPV 5553 | 3.1* | | 3.5* | | 3.7* | | 4.4* | | | | | |

*measurement approximate

compared to M2 (M2/3 in *Tremacyllus* are similar in size), and P2 that is relatively longer mesiodistally and triangular in occlusal outline (P2 of *Tremacyllus* is roughly circular). PACH B is similar in size to *Paedotherium minor*; P3-4 in both taxa are roughly triangular in outline (although P3-4 of PACH B are wider labiolingually than their counterparts in *Paedotherium minor*). PACH B is distinguished from all species of *Paedotherium* (including *P. minor*) by its small M3 (in *Paedotherium* M3 is often larger than M2) and long P2 (in PACH B, P2-3 are nearly equally long mesiodistally, while in *Paedotherium* P2 is significantly shorter than P3).

DESCRIPTION: PACH B (fig. 3.5) represents a medium-sized pachyrukhine, comparable in tooth dimensions to *Paedotherium minor*.

I1 is very large – mesiodistally long but labiolingually narrow – and curved along the contour of the rostrum. A large diastema separates I1 and P2. P2, relatively long mesiodistally (similar in length to P3) but narrow labiolingually, is triangular in occlusal outline. The labial wall of P2 bears a vertical paracone column which is separated from the parastyle by a shallow vertical trough. P3/4 are approximately the same length (mesiodistally) as P2, and are also fairly triangular in occlusal outline, but they are much wider labiolingually than P2. The lingual margin of P4 is slightly more convex than the straight lingual margin of P3, making P4 a more robust tooth. The lingual wall of P4 is marked by a shallow vertical sulcus (near the posterolingual corner of the tooth); a faint trace of this sulcus also appears on P3, but would have disappeared completely after little wear (perhaps on P4, as well). Other pachyrukhines, e.g. *Pachyrukhos* (personal obs.), are also inferred to lose this sulcus through wear. The labial wall of P3 is relatively flat, but a small, vertical paracone column occurs on P4, anterior of which is another column associated with the parastyle. M1 and M2 are very similar, but M1 is slightly larger (making it the largest

cheek tooth). Both anterior molars are roughly trapezoidal in occlusal outline, but with rounded edges. The lingual margins of these teeth are completely flat and continuous. The posterior margin of M1 is somewhat broader (labiolingually) than on M2. The labial wall of M1 bears three distinct and adjacent columns, the posterior of which occurs near the middle of the tooth, the middle one is associated with the paracone, and the anterior one is associated with the parastyle. M2 possesses two of these vertical columns along its labial wall (a paracone column and a column directly posterior to it), but lacks a parastyle column. M3 is significantly smaller than the anterior molars, and has a more rounded lingual margin, making the tooth semicircular in occlusal outline. Compared to P4-M2, the labial wall of M3 is relatively smooth and flat.

REMARKS: A preliminary analysis initially identified SGOPV 3805 as *Paedotherium minor* (Flynn *et al*., 2008, fig. 4g). Although SGOPV 3805 certainly resembles *Paedotherium minor* in some respects (most notably, in size and subtriangular P3-4), in other respects this specimen lacks the diagnostic features of the *Paedotherium* altogether (M3 of SGOPV 3805 is relatively short and P2 is long, whereas *Paedotherium* is diagnosed by a relatively long M3 and short P2; see Cerdeño and Bond, 1998). Herein we identify closer similarities between SGOPV 3805 and *Pachyrukhos moyani* Ameghino, 1885. In fact, the only notable differences between the two are that the P3-4 of SGOPV 3805 are labiolingually wider and triangular in occlusal outline (in *Pachyrukhos moyani* P3-4 are significantly narrower and trapezoidal; see fig. 3.6b-c) and P4-M2 bear distinct labial ridges separated by distinct grooves (some specimens of *Pachyrukhos* bear subtle labial grooves on the cheek teeth, but the ridges and grooves of PACH B are much more pronounced).

Similarities between SGOPV 3805 and *Pachyrukhos moyani* are sufficient to have made us to consider assigning SGOPV 3805 to a new species of *Pachyrukhos* (Luna *et al*.,

2011, 2013). Instead, we designate SGOPV 3805 as the holotype of Pachyrukhinae gen. *et* sp. *nov*. B, for the following reasons: 1) Late-diverging pachyrukhines (*Pachyrukhos*, *Tremacyllus*, *Paedotherium*) are differentiated from each other mainly by fairly subtle aspects of the dentition (e.g., size of P2 and M3, imbrication of cheek teeth, outline shape of premolars; see Cerdeño and Bond, 1998). The dental features distinguishing PACH B from *Pachyrukhos* (and other taxa) are similar in heft and validity as those considered diagnostic of other late-diverging pachyrukhine genera. 2) *Pachyrukhos*, *Tremacyllus*, and *Paedotherium* are diagnosed by cranial characteristics that currently cannot be determined in PACH B, as this taxon is known almost exclusively from upper dentition. Clearly, absence of evidence has no bearing on our recognition of a new genus, but it does complicate the possible assignment of these specimens to *Pachyrukhos*. 3) The phylogenetic results of the present study do not support a particularly close relationship between PACH B and *Pachyrukhos*. In the strict consensus tree (figs. 3.8, 3.9) PACH B, *Pachyrukhos*, *Tremacyllus*, and *Paedotherium* are nested within a single polytomy. In fact, PACH B and *Pachyrukhos* are not resolved as sister taxa in either of the two equally parsimonious trees from which the consensus is determined. The typologies of these two trees suggest that the similarities between *Pachyrukhos* and PACH B are either plesiomorphic (PACH B, (*Pachyrukhos*, (*Tremacyllus*, *Paedotherium*))) or convergent (*Pachyrukhos*, (*Paedotherium* (*Tremacyllus*, PACH B))). Given the lack of evidence that PACH B and *Pachyrukhos* form a distinct clade, proposing that PACH B represents a new species within *Pachyrukhos* would be ill-advised, despite their similarities. 4) *Pachyrukhos* is long overdue for taxonomic revision. Although such an effort is well beyond the scope of this study, we offer a few preliminary observations:

- Sinclair's (1909) revision remains the most thorough and useful treatment of *Pachyrukhos*. It assesses relatively few taxa – only *P. moyani* is recognized as valid (*P. naevius* and *P. absis* are regarded as junior synonyms); *P. teres* and *P. trivius* are considered Typotheria *incertae sedis*.
- We examined several specimens of *P. teres* at the MACN and MLP, including two labeled as "syntypes" (MACN-A 262 and MACN-A 297), and although some of these specimens are slightly smaller than *P. moyani*, they are in all other respects extremely similar. Some specimens of *P. teres* show a higher degree of imbrication between P3-M1, but this feature likely varies with age. We suggest *P. teres* may be synonymous with *P. moyani*.
- We examined several specimens of *P. trivius* at the MACN and MLP, but could not identify a type specimen. Much of this material appears to be referable to *P. moyani*, but some specimens may pertain to other taxa, as well. Unfortunately, most of this material is difficult to confidently assess, as most specimens consist of two or three teeth lacking diagnostic morphology.
- In addition to the above taxa, Ameghino (1887a, 1887c, 1888, 1889, 1902, 1908) described at least 11 other species of *Pachyrukhos* (most originally described as *Pachyrucos*). Ten of these (and one subspecies described by Rovereto [1914]) were synonymized with *Tremacyllus impressus*, *Paedotherium typicum*, or *P. bonaerense* (Cerdeño and Bond, 1998). Despite this thorough revision, no emended diagnosis of *Pachyrukhos* has been proposed.
- To our knowledge, *Pachyrucos politus* (Ameghino, 1902), from Ameghino's "couches à Colpodon" (=Colhuehuapian), has not been synonymized. Our

examination of MACN-A 53-438 (labeled as the holotype; right mandible bearing p2-m3) suggests that this specimen is likely assignable to a different genus altogether. These lower teeth are larger than those of *P. moyani*, and p2, which is subequal in size to p3-m2, bears a well-developed trigonid and salient labial sulcus. Conversely, p2 in *P. mayoni*, *Tremacyllus*, and *Paedotherium* is relatively small, with a poorly developed trigonid and a labial sulcus that is small or absent. In these respects, MACN-A 53-438 ("*Pachyrucos politus*") most closely resembles *Propachyrucos* and *Prosotherium*. Until a more complete revision is realized, MACN-A 53-438 should be considered Pachyrukhinae *incertae sedis*.

- Roth (1898) described three species of *Propachyrucos* – *P. depressus*, *P. medianus*, and *P. robustus* – that Pascual *et al*. (1978) reassigned to different species of *Pachyrukhos*. Their type specimens (MLP 12-2915 for *P. depressus*; MLP 12-3160 for *P. medianus*; MLP 12-3161 for *P. robustus*) are limited to a few teeth, bearing little (if any) diagnostic morphology. We cannot confidently attribute these specimens to any particular species or genus of pachyrukhine. Accordingly, these specimens should be considered Pachyrukhinae *incertae sedis*.
- This brief taxonomic assessment suggests that *Pachyrukhos moyani* may be the only valid species of *Pachyrukhos*.

Given the available evidence and current understanding of pachyrukhine taxonomy, we recognize SGOPV 3805 and SGOPV 3953 as a new genus and species. It is important to emphasize the close similarity between these LdL specimens and *P. moyani*; additional specimens (especially preserving cranial morphology), future phylogenetic analyses, and a

long-overdue revision of *Pachyrukhos* may motivate future researchers to re-evaluate the taxonomy proposed here.

## Pachyrukhinae indeterminate

**SGOPV 3970 (cf. *Pachyrukhos moyani*)**. SGOPV 3970 consists of a partial skull and mandible bearing left M1-3/m1-3 in occlusion (M1/m1 broken); both upper and lower molars can be readily examined in labial view, but a limited occlusal view of these teeth is also available. Portions of the left side of the skull, posterior to the first molar, are preserved, including fragments of the maxilla, jugal, lacrimal, frontal, and parietal; part of the body of the mandible (below m1-3) and the ascending ramus are also preserved. This specimen was recovered from Estero Campamento (site C-04-32) within unit $Tcm_3$ of the Cura-Mallín Formation (Herriott, 2006) (figs. 3.1, 3.2). Although the stratigraphic position of site C-04-32 is only moderately constrained, it is confidently bracketed by two ignimbrites dated to 16.40 ± 0.30 Ma (CH-5) and 17.90 ± 0.40 Ma (CH-15) (fig. 3.2).

SGOPV 3970 is undoubtedly affiliated with the clade of post-Oligocene pachyrukhines (PACH B, *Pachyrukhos*, *Paedotherium*, *Tremacyllus*), based on its small size, trilobed m3 (character 18, state 2), flat lingual wall of the upper molars (character 9, state 1), extremely large orbit (character 22, state 1), and lack of sagittal crest (character 26, state 2). Unfortunately, presently available diagnostic information precludes confident referral to any known genus or species. Nevertheless, we can confidently rule out referral to some taxa: SGOPV 3970 is larger than *Tremacyllus* and its M3 is mesiodistally shorter than in *Paedotherium* (in *Paedotherium*, M3 is mesiodistally longer than M2, while in SGOPV

3970 the reverse is true). Although secure diagnostic information is limited, SGOPV 3970 is very similar in size and known morphology to *Pachyrukhos moyani*. In turn, *P. moyani* is generally very similar to PACH B (see Remarks in Systematic Paleontology): PACH B is most readily distinguished from *P. moyani* by the former's wider, triangular P3-4 (these teeth are not preserved in SGOPV 3970) and salient labial ridges separated by distinct grooves on P4-M2 (SGOPV 3970 preserves M1-2). Even though SGOPV 3970 was recovered from horizons similar in age to those from which PACH B derives (fig. 3.2), we exclude this specimen from the PACH B hypodigm primarily because it lacks the distinct labial ridges that characterize P4-M2 of SGOPV 3805 and SGOPV 3953 (specimens herein referred to PACH B). SGOPV 3970 does exhibit subtle labial grooves on M1-2, a condition also seen in *Pachyrukhos moyani*. This distinction (shallow grooves vs. salient ridges separated by deeper grooves) is not profound, underscoring our lack of confidence in identifying this specimen. It is possible, for example, that the degree to which these labial ridges/grooves are expressed is variable in PACH B, and that SGOPV 3970 may, indeed, pertain to the same taxon. This question can only be resolved through the recovery of additional material. In the meantime, we offer the following additional observations: Although preservation is less than ideal, approximate measurements for SGOPV 3970 are: M2 mesiodistal length – 4.9 mm; M3 mesiodistal length – 4.4 mm; mandible height (below p1 talonid) – 11.82 mm; size of orbit (measured from the lacrimal-jugal suture to the tip of the postorbital process) – 20.1 mm.

M2-3 mesiodistal lengths provide the only direct size comparison between SGOPV 3970, PACH B, and *Pachyrukhos*. A plot of M2/3 mesiodistal lengths (fig. 3.7) shows that SGOPV 3953 falls within the upper size range of *P. moyani*, whereas PACH B falls near (or below, in the case of M3) the lower size range of *P. moyani*.

The age constraints of SGOPV 3970 (~16.5-18 Ma) overlap with the known distribution of *P. moyani*, a taxon best known from coastal exposures of the Santa Cruz Formation (Ameghino, 1885, 1887a, 1889; Sinclair, 1909) that likely range in age from 18-16 Ma (Marshall *et al*., 1986; Fleagle *et al.*, 1995; Perkins *et al*., 2012).

Based on the available data and current taxonomy, SGOPV 3970 seems more closely affiliated with *P. moyani* than PACH B.

**SGOPV 5553.** This specimen consists of a partial skull and mandible bearing left i-2 and left P2-M3 in tight occlusion with the lower cheek teeth. Because the teeth are clenched, the lower dentition cannot be examined, and only the labial faces of P2-M2 can be readily viewed (although a limited view of the occlusal surface of these teeth is available). Small fragments of the maxilla and jugal are preserved; although much of the body of the mandible and a small part of the ascending ramus is present, they are highly eroded, obscuring the true size of the mandible. Several displaced tooth fragments also occur in the surrounding matrix. SGOPV 5553 was recovered from site C-05-6; although there is some uncertainty regarding the location of this site, it occurs within the Trapa Trapa East collecting region, probably within the upper third of unit $Tcm_1$ of the Cura-Mallín Formation (Herriott, 2006) (figs. 3.1, 3.2). Although its stratigraphic position is imprecise, it is bracketed by an underlying ash-fall tuff dated to 19.5 ± 0.60 Ma and an overlying ignimbrite dated to ~18 Ma (two samples from this ignimbrite yield ages of 18.00 ± 0.30 Ma [sample CH-13a] and 17.84 ± 0.24 Ma [CH-24]) (fig. 3.2).

Several features suggest that SGOPV 5553 is closely related (or belongs) to the minimally inclusive clade comprising post-Oligocene pachyrukhines (PACH B, *Pachyrukhos*, *Paedotherium*, *Tremacyllus*), including its small size, the absence of P1

(character 6, state 1), the flat lingual wall of M1 (character 9, state 1), and an i1 that is significantly larger than i2 (character 14, state 1).

SGOPV 5553 is clearly smaller than SGOPV 3970, but, due to incomplete preservation, they cannot be directly compared with precise measurements (i.e., both specimens possess M1 and M2, but M1 of 3970 is broken, and M2 of 5553 is obscured in a manner preventing accurate measurement). Based on the approximate mesiodistal lengths of P2-M1, SGOPV 5553 is most comparable in size to PACH B (table 3.3) and *Paedotherium* (see tables 3-4 in Cerdeño and Bond, 1998); these two taxa are readily distinguished by the width of P3-4 and the size of P2 and M3 (i.e., P3-4 of PACH B are relatively wider labiolingually; P2-3 of PACH B are similar in mesiodistal length, but P2 of *Paedotherium* is shorter than P3; M3 of PACH B is notably smaller than M2, but M3 of *Paedotherium* is either larger than or subequal in size to M2). In SGOPV 5553, however, the width of P3-4 and size of M3 are obscured by their tight occlusion with the lower teeth, so these diagnostic characters cannot be examined. The mesiodistal length of P2 (compared to P3) is also of limited use because these measurements in SGOPV 5553 are approximate (again, due to the tight occlusion), and we are uncertain about the true range of P2 size in PACH B, since this taxon is only known from two specimens. With these limitations in mind, we tentatively suggest that, in SGOPV 5553, the mesiodistal length of P2 is more similar to that of PACH B than *Paedotherium*. Given its lack of salient labial ridges and grooves on P4-M2, we are reluctant to refer SGOPV 5553 to PACH B.

In view of the above considerations, we suggest four alternative interpretations. SGOPV 5553 represent either: 1) a new pachyrukhine genus, 2) an abnormally small specimen of *Pachyrukhos*, 3) a very early occurrence of *Paedotherium* in which P2 is not as reduced with respect to P3 as in later known taxa (Chasicoan-Marplatan), or 4) a specimen

of PACH B lacking the pronounced labial ridges and grooves seen in SGOPV 3805 and SGOPV 3953. The fourth option would require slight emendation of the diagnosis of PACH B provided above. Given the dearth of diagnostic morphology in SGOPV 5553, discriminating between these options requires additional data and fossil material.

## PHYLOGENETIC CONSIDERATIONS

The description of two new taxa from the LdL region of Chile provides an opportunity to reexamine and expand upon several previous studies of hegetotheriid relationships (e.g., Cifelli, 1993; Cerdeño and Bond, 1998; Croft and Anaya, 2006; Billet *et al*., 2009; Billet, 2010, 2011; Reguero and Prevosti, 2010; Kramarz and Paz, 2013). Many of these analyses focused on the relationships between hegetotheriids, archaeohyracids, mesotheriids, and other typotherian notoungulates (e.g., Cifelli, 1993 Billet *et al*., 2009; Billet, 2010; Reguero and Prevosti, 2010; Kramarz and Paz, 2013); here we limit our focus to relationships *within* Hegetotheriidae (as in Cerdeño and Bond, 1998; Croft and Anaya, 2006), although we also discuss our choice of an appropriate outgroup.

Beginning with the groundbreaking cladistic studies of Cifelli (1993), support for hegetotheriid monophyly has been consistent (Billet *et al*., 2009; Billet, 2010, 2011; Reguero and Prevosti, 2010; Kramarz and Paz, 2013). Several studies employ the paraphyletic archaeohyracids (or *Archaeohyrax* alone) as the outgroup to Hegetotheriidae (Cifelli, 1993; Croft *et al*. 2003; Croft and Anaya, 2006), an arrangement first suggested taxonomically by Simpson (1967). Mesotheriids have also been considered the proximal outgroup to hegetotheriids, with archaeohyracids representing a paraphyletic assemblage outside that

pairing (Reguero and Prevosti, 2010). Finally, two recent studies view a clade of "late archaeohyracids" (*Archaeotypotherium*, (*Protarchaeohyrax*, *Archaeohyrax*)) as the hegetotheriid outgroup, with mesotheriids diverging earlier but *within* the paraphyletic archaeohyracids (Billet *et al*., 2009; Kramarz and Paz, 2013). Considering the long history of using archaeohyracid outgroups to elucidate hegetotheriid relationships (Cifelli, 1993; Billet *et al*., 2009; Billet, 2010; Croft and Anaya, 2006; Kramarz and Paz, 2013), we follow Billet *et al*. (2009) and Kramarz *et al*. (2013) and employ the "late archaeohyracid clade" as our hegetotheriid outgroup, determining outgroup character states by reconstructing the ancestral character states of this clade. Should future phylogenetic analyses further support a clade composed exclusively of Hegetotheriidae + Mesotheriidae, the resulting differences in outgroup character states would not be significant, since both the "late achaeohyracid clade" and the earliest diverging mesotheriids (e.g., *Trachytherus*) possess morphologies that are similarly plesiomorphic with respect to hegetotheriids.

Little consensus exists regarding intra-hegetotheriid relationships, each new study offering divergent interpretations (compare Cifelli, 1993; Cerdeño and Bond, 1998; Croft and Anaya, 2006; Billet *et al*., 2009; Billet, 2010, 2011; Reguero and Prevosti, 2010; Kramarz and Paz, 2013). Perhaps the only consistent and well-supported feature of hegetotheriid relationships is the monophyly of Pachyrukhinae (Cerdeño and Bond, 1998; Croft and Anaya, 2006; Billet *et al*., 2009; Billet, 2010, 2011; Reguero and Prevosti, 2010; Kramarz and Paz, 2013). Our phylogenetic results corroborate pachyrukhine monophyly, and are consistent with Reguero and Prevosti's (2010, p. 156) proposal that "Pachyrukhinae could potentially be defined as the MRCA of *Propachyrucos* and *Paedotherium* and all of its descendants." A persistent question concerns the monophyly (Billet *et al*., 2009; Kramarz

and Paz, 2013[2]) or paraphyly (Croft and Anaya, 2006; Reguero *et al*., 2007; Reguero and Prevosti, 2010) of Hegetotheriinae.

Here we seek to advance the study of hegetotheriid relationships by incorporating new taxa (both from LdL and from recent publications) and by coding these taxa for a greater number of informative characters (combined from recent studies and incorporating new observations). In addition to incorporating all taxa analyzed by Kramarz and Paz (2013), we make the following additions and modifications: 1) we include HEG A and PACH B, the two new taxa from LdL; 2) we include *Medistylus*, which Reguero *et al*. (2007) recently redescribed based on new material, but has only been incorporated in just one phylogenetic analysis previously (Reguero and Prevosti, 2010) (we did not have access to specimens of this taxon; our coding is based on the figures and descriptions in Reguero *et al*. [2007] and the dataset of Reguero and Prevosti [2010]); 3) we code several pachyrukhine taxa separately, including *Prosotherium*, *Propachyrcos*, *Pachyrukhos*, *Tremacyllus*, and *Paedotherium* (as in Cerdeño and Bond, 1998; Croft and Anaya. 2006; Reguero and Prevosti, 2010); 4) we code *Hemihegeotherium trilobus* separately from other species of *Hemihegetotherium* (as in Croft *et al*., 2006), primarily because *H. trilobus* and HEG A both possess a trilobed m3, and a close relationship between these taxa could challenge the monophyly of *Hemihegetotherium*. The 36 characters used in this phylogenetic analysis primarily represent a combination of datasets from Croft *et al*. (2006) and Billet *et al*. (2009) (the latter dataset was also used by Kramarz and Paz [2013]); new observations and

[2] In the phylogenetic analysis of Kramarz and Paz (2013), hegetotheriines are considered monophyletic, but with qualifications concerning clade membership: Hegetotheriinae includes *Hegetotherium mirabile*, *Hemihegetotherium*, *Prohegetotherium*, and *Sallatherium*, but excludes "*Hegetotherium*" *novum* (which the authors suggest should be assigned to a new genus) and *Hegetotheriopsis sulcatus*.

characters are also incorporated. Appendix 3.2 provides a detailed character list, highlighting similarities and differences with respect to previous studies. A total of 17 hegetotheriid taxa are coded for 36 characters; this is the largest character matrix yet assembled exclusively for Hegetotheriidae.

Several features of our phylogeny merit discussion. Consistent with all recent studies of hegetotheriid relationships (Cerdeño and Bond, 1998; Croft and Anaya, 2006; Billet *et al*., 2009; Reguero and Prevosti, 2010; Kramarz and Paz, 2013), our results strongly support pachyrukhine monophyly (figs. 3.8, 3.9). Although the topology of intra-pachyrukhine relationships favored here (see below) differs from that of Reguero and Prevosti (2010), the membership of Pachyrkhinae, defined as "the MRCA of Propachyrucos and *Paedotherium* and all of its descendants" (Reguero and Prevosti, 2010, p. 156), is congruent between the two studies. One limitation of this definition is that *Paedotherium* may be paraphyletic (Reguero and Prevosti, 2010), so we propose a slight clarification, defining Pachyrkhinae as "the MRCA of *Propachyrucos* and *Paedotherium bonaerense* and all of its descendants." Compared to previous efforts, however, our analysis suggests significant differences with respect to relationships *within* Pachyrukhinae. All previous studies (Cifelli, 1993; Cerdeño and Bond, 1998; Croft and Anaya, 2006; Reguero and Prevosti, 2010), pair *Propachyrcos* and *Prosotherium* as an early (Deseadan) outgroup to the post-Oligocene pachyrukhines (*Pachyrukhos*, *Tremacyllus*, *Paedotherium*). Reflecting this consensus, Billet *et al*. (2009) and Kramarz and Paz (2013) coded *Propachyrukhos-Prosotherium* as a single taxon in their analyses. Conversely, our results indicate that *Propachyrcos*, *Medistylus*, and *Prosotherium* represent a paraphyletic assemblage of early-diverging pachyrukhines. This arrangement has

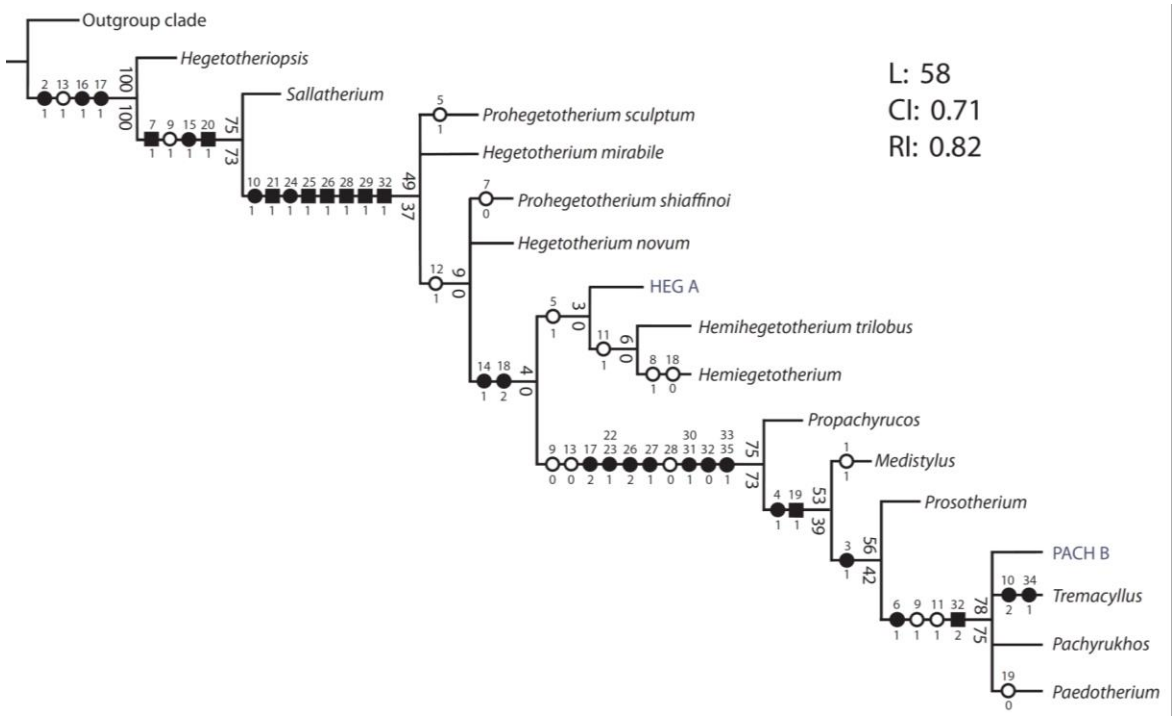


FIGURE 3.8. Strict consensus tree of Hegetotheriidae. "Outgroup clade" includes *Archaeotypotherium*, *Protarchaeohyrax*, and *Archaeohyrax*, based on the phylogenetic analyses of Billet et al. (2009) and Kramarz et al. (2013). Synapomorphies indicated by circles or squares, with character numbers above and character states below (see appendix 1 for character descriptions). Squares indicate an equivocal condition in which the outgroup to the clade is missing data for that character. Open squares and circles are homoplasies. At the base of each node are the confidence scores from symmetric resampling (absolute frequencies above; relative frequencies below). Abbreviations: L, length; CI, consistency index; RI, retention index.

two favorable implications: 1) the earliest pachyrukhines (represented here by *Propachyrcos*) possessed at least vestigial I2-C/i3-c (characters 3 and 4; fig. 3.8; appendices 3.2 and 3.3), inheriting a full dental formula from their hegetotheriid ancestors; and 2) later-diverging, Deseadan pachyrukhines (*Medistylus*, *Prosotherium*) progressively lost I2-C/i3-c, with post-Oligocene pachyrukhines (PACH B, *Pachyrukhos*, *Tremacyllus*, *Paedotherium*) also eventually losing P1/p1. On the other hand, earlier studies resolving *Propachyrcos* and *Prosotherium* as a clade (Cifelli, 1993; Cerdeño and Bond, 1998; Croft and Anaya, 2006; Reguero and Prevosti, 2010) required dental reduction to have occurred independently within two pachyrukhine lineages, with the complete loss of several teeth in post-Oligocene taxa being unrelated to the gradual reduction of teeth in Deseadan taxa. Considering these

alternatives for dental reduction, our topology is certainly preferable. Of course, previous studies supporting the monophyly of *Propachyrcos* and *Prosotherium* offer other advantages; our results, by comparison, require an additional, convergent loss of the upper molar lingual sulcus in post-Oligocene pachyrukhines (character 9, state 1). Even if there is little *a priori* reason to favor either of these interpretations, our goal is to highlight a new hypothesis for pachyrukhine morphological evolution.

One unfortunate limitation of our phylogeny is the polytomy of the clade comprising post-Oligocene pachyrukhines (PACH B, *Pachyrukhos*, *Tremacyllus*, *Paedotherium*). The uncertainty of these relationships was also reflected in the landmark revision of Cerdeño and Bond (1998), where three equally parsimonious phylogenies suggested alternate positions for *Pachyrukhos*, *Tremacyllus*, and *Paedotherium*. One of these topologies (*Pachyrukhos*, (*Tremacyllus*, *Paedotherium*)) has since been supported by Croft and Anaya (2006), but Reguero and Prevosti (2010) found that *Tremacyllus impressus* nested within *Paedotherium*, making the latter genus paraphyletic. Given this lack of consensus and the ambiguity of our own results, we emphasize that these relationships remain an open question. Further, considering the results of Reguero and Prevosti (2010), it is likely that future phylogenetic analyses can be improved by treating each species of *Tremacyllus* and *Paedotherium* as separate taxa (PACH B and *Pachyrukhos* are both likely monospecific – see Remarks in PACH B Systematic Paleontology).

Another important feature of our phylogenetic analysis is the paraphyly of "Hegetotheriinae." In this respect, our results generally support the conclusions of Croft and Anaya (2006) and Reguero and Prevosti (2010), contrasting with studies favoring hegetotheriine monophyly (Billet *et al*., 2009; Kramarz and Paz, 2013). Our preferred phylogeny particularly resembles that of Croft and Anaya (2006) in *Hemihegetotherium*

resolving as the outgroup to Pachyrukhinae. Our results build on this conclusion, suggesting that HEG A and *Hemihegeotherium* form a clade, which together represent the outgroup to Pachyrukhinae. Two synapomorphies diagnose the HEGA + *Hemihegetotherium* + Pachyrukhinae clade: i1 is significantly larger than i2 (character 15, state 1) and the m3 talonid bears a strong labial sulcus, making this tooth distinctly trilobed (character 18, state 2). According to this topology, the trilobed m3 was lost in some species of *Hemihegetotherium* (character 18, state 2) (still, the monophyly of *Hemihegetotherium* is supported). As discussed previously, we are convinced HEG A possesses a trilobed m3, but this understanding is based on specimens that were not found in direct association. Therefore, we also conducted a preliminary analysis excluding lower molar morphology for HEG A; although minor differences in the position of more basal hegetotheriids result, it is notable that the same topology for HEG A + *Hemihegetotherium* + Pachyrukhinae is supported, increasing our confidence in these results.

Even in studies recognizing "Hegetotheriinae" as paraphyletic (Croft and Anaya, 2006; Reguero and Prevosti, 2010), there remains much uncertainty regarding the phylogenetic position of early-diverging taxa, such as *Sallatherium*, *Prohegetotherium*, and *Hegetotherium*. Indeed, one recent study (Kramarz and Paz, 2013) highlights a potential problem underlying this lack of resolution: *Hegetotherium* and *Prohegetotherium* may actually be non-monophyletic. Our results, while differing significantly from those of Kramarz and Paz (2013), also suggest that *Hegetotherium* and *Prohegetotherium* are not monophyletic, with *Prohegetotherium schiafinnoi* and *Hegetotherium novum* nested in one polytomy, and *Prohegetotherium sculptum* and *Hegetotherium mirabile* nested in an earlier-diverging polytomy (fig. 3.8). These results underscore the need for taxonomic revision of these genera.

*Sallatherium* and *Hegeotheriopsis* are the most basal taxa in our phylogeny. The position of *Sallatherium* has varied considerably in previous studies (compare Billet *et al*., 2009; Reguero and Prevosti, 2010; Kramarz and Paz, 2013); we feel that a basal position for *Sallatherium* is warranted by several plesiomorphic characters, especially with regard to skull morphology (see fig. 3.8 and appendices 3.2 and 3.3). *Hegetotheriopsis*, recently described (Kramarz and Paz, 2013), has been proposed to occupy the most basal position within Hegetotheriidae, an interpretation affirmed by our results. The dental morphology of *Hegetotheriopsis* is plesiomorphic with respect to later-diverging hegetotheriids in that the upper and lower molars bear distinct lingual sulci (character 9, state 0; character 15, state 0).

The phylogenetic position of *Hegetotheriopsis* and *Sallatherium* has implications for the definition of Hegetotheriidae. The monophyly of Hegetotheriidae has been consistently well supported (Cifelli, 1993; Billet *et al*., 2009; Reguero and Prevosti, 2010; Kramarz and Paz, 2013), leading Reguero and Prevosti (2010, p. 156) to suggest that "Hegetotheriidae could potentially be defined as the MRCA of *Prohegetotherium* (the most basal member of the clade) and *Paedotherium* (or any other hegetotheriid) and all of its descendants." Applied to the present study, this definition would exclude *Sallatherium* and *Hegetotheriopsis*; applied to the results of Kramarz and Paz (2013), *Hegetotherium novum* and *Hegetotheriopsis* would be excluded. All these excluded taxa were originally described as hegetotheriids (Bordas, 1939; Reguero and Cerdeño, 2005; Kramarz *et al*., 2013), and *Sallatherium* in particular has been consistently regarded as a hegetotheriid (Reguero and Cerdeño, 2005; Croft and Anaya, 2006; Billet *et al*., 2009; Reguero and Prevosti, 2010; Kramarz and Paz, 2013). Moreover, *Prohegetotherium*, which Reguero and Prevosti [2010] use as a bracketing taxon in their definition of Hegetotheriidae, may not be monophyletic (Kramarz and Paz, 2013; this study). Clearly, a preferable definition of Hegetotheriidae will

recognize the membership of taxa originally described and consistently regarded as hegetotheriiids, and provide increased stability with regard to the membership of the clade. Considering the instabilities in recent phylogenetic analyses of hegetotheriids, we propose a "stem-based" (de Queiroz and Gauthier, 1990, 1992) definition: Hegetotheriidae is the clade composed of all taxa that are more closely related to *Paedotherium bonaerense* than they are to Mesotheriidae, *Archaeotypotherium*, *Protarchaeohyrax*, or *Archaeohyrax*. Using this definition, the present study identifies the following hegetotheriid synapomorphies: hypselodont cheekteeth (character 2, state 1), M3 reduced in size (character 13, state 1), lower molars bearing a deep labial sulcus (character 16, state 1), and m1-2 exhibiting a regular shape throughout wear, with labially rounded trigonid and talonid lobes (character 17, state 1).

Undescribed (and mostly fragmentary) hegetotheriid specimens are reported from as early as the Tinguiririan SALMA in Chubut Province, Argentina (Reguero, 1993, 1999; Flynn *et al*., 2003; Dozo *et al*., 2014) and Chachapoal in central Chile (Croft *et al*., 2008),[3] but the hegetotheriid fossil record is not well known until the Deseadan SALMA (Ameghino, 1897; Loomis, 1914; Simpson, 1945b; Marshall *et al*., 1983; Reguero and Cerdeño, 2005; Reguero *et al*., 2007), with at least six taxa recognized from this interval (fig 3.9.). This proliferation of Deseadan hegetotheriids almost certainly corresponds to the

[3] *Ethegotherium carettei* was previously thought to represent the oldest hegetotheriid. This taxon, originally described as *Prohegetotherium caretti* (Minoprio, 1947), was later assigned to the genus *Ethegotherium* (Simpson *et al*., 1962). Partly based on the supposed occurrence of this taxon in the Divisadero Largo Formation, Pascual *et al*. (1965) proposed the establishment of the "Divisaderan" SALMA, corresponding to the late Eocene. Subsequent studies have found that *Ethegotherium carettei* is synonymous with *Prohegetotherium schiaffinoi* (Reguero and Cerdeño, 2005), and that these supposedly "Divisaderan" specimens of *P. schiaffinoi* belong to the overlying Mariño Formation (Cerdeño *et al*., 2008). Although the age of the Mariño Formation is not precisely known, biostratigraphic evidence suggests a late Oligocene or early Miocene age (Cerdeño *et al*., 2006, 2008).

development of hypselodonty in this clade (character 2, state 1) (figs. 3.8, 3.9). Our analysis further indicates that many later-diverging taxa also have their roots in this Deseadan radiation (fig. 3.9); a similar trend has recently been observed among hypselodont interatheriines (Ch. 2). These clades of small-bodied typotherians convergently acquired hypselodont dentition, likely in the early to middle Oligocene, leading to simultaneous radiations in the Deseadan.

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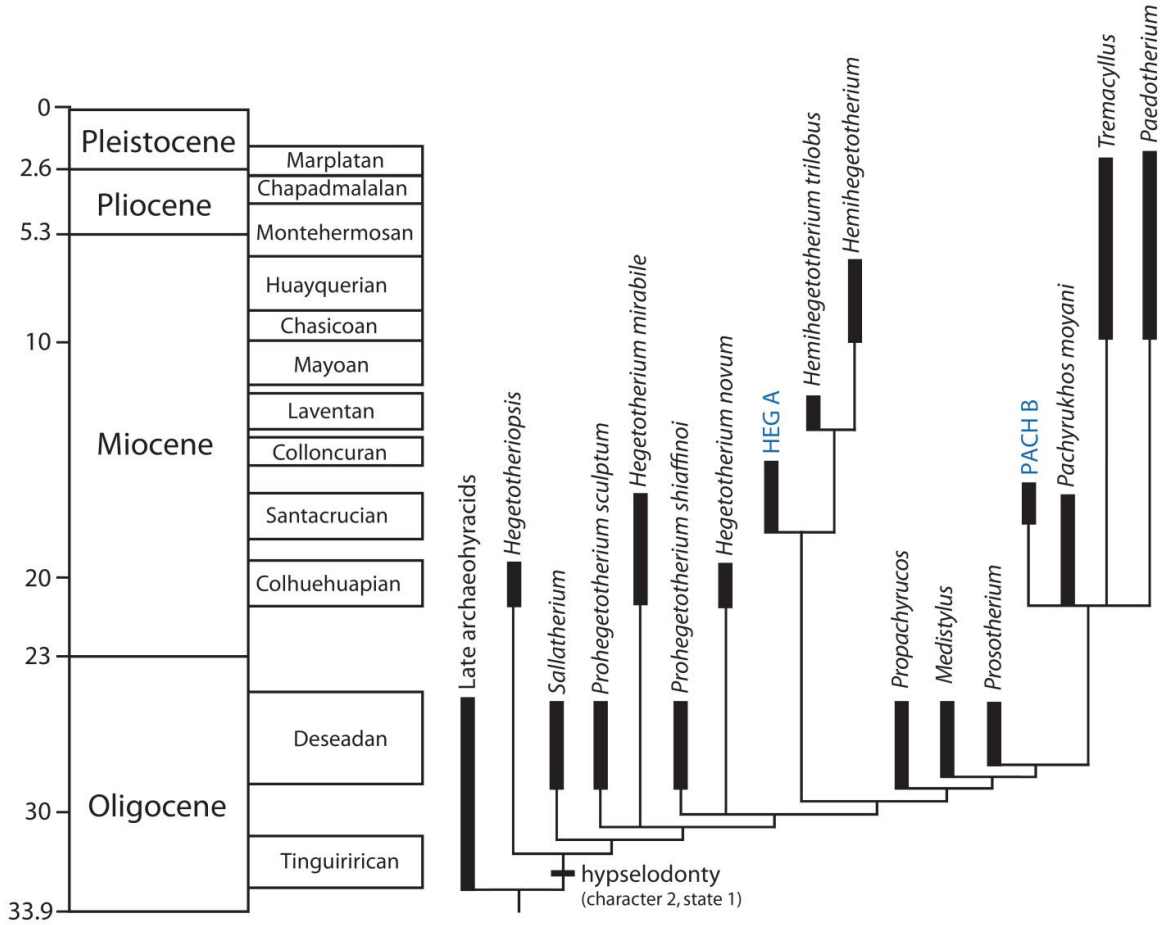


FIGURE 3.9. Phylogeny of Hegetotheriidae, with the temporal range of each taxon indicated by black bars. "Late achaeohyracids" (outgroup) include *Archaeotypotherium*, *Protarchaeohyrax*, and *Archaeohyrax*.

## SUMMARY AND CONCLUSIONS

Above we have described hegetotheriid fossils recovered from Miocene-aged exposures of the Cura-Mallín Formation, southeast of Laguna del Laja, in the Andes of central Chile. These fossils include two newly described taxa, ranging in age from ~15-18 Ma (early to middle Miocene), and representing the first novel hegetotheriid taxa described from Chile. Incorporating these new taxa, we expand upon previous analyses of hegetotheriid relationships. Our findings include:

**HEG A**: Hegetotheriidae *gen*. et *sp*. nov. A (herein referred to as HEG A) is described on the basis of three specimens – SGOPV 3806 (the holotype, from Estero Trapa Trapa East), SGOPV 3891 (from Estero Campamento), and SGOPV 3934 (from Cerro los Pinos) – the stratigraphic positions of which correspond to an age range of ~15.2-18 Ma. The diagnosis and description of HEG A is based primarily on the holotype, which includes the complete left C-M3 and partial I2-3 (we assume I1 was present but not preserved). HEG A is a relatively small "hegetotheriine," similar in size to *Prohegetotherium schiaffinoi*, but with the roughly rectangular upper molars that characterize *Hegetotherium*. Our phylogenetic analysis indicates that HEG A is sister-taxon to *Hemihegetotherium*, these taxa being united by a single synapomorphy: the upper canine root is positioned labially with respect to P1 (character 5, state 1). Compared to *Hemihegetotherium*, HEG A is easily distinguished by its significantly smaller size, its P4-M3 being much more rectangular in outline, and by possessing a diastema between I2/3. HEG A is further distinguished from all other hegetotheriids in having an unusually large P1 (fig. 3.4). Although based on somewhat circumstantial evidence, we are confident in assigning SGOPV 3891 and 3934 to HEG A. These specimens include one upper cheektooth (M1?) and several lower cheekteeth (?p4,

m2-3). The most notable feature of the lower dentition is the trilobed m3, which evidently allies HEG A with *Hemihegetotherium trilobus* and pachyrukhines.

**PACH B**: Pachyrukhinae *gen*. et *sp*. nov. B (herein referred to as PACH B) is described on the basis of two specimens (SGOPV 3805 and SGOPV 3953) recovered from Trapa Trapa West, ranging in age between ~15.6-17.4 Ma. Known from a complete upper dental series, PACH B is clearly affiliated with post-Oligocene pachyrukhines (*Pachyrukhos*, *Tremacyllus*, *Paedotherium*); all these taxa have molars with continuous lingual margins and lack any trace of I2-P1. PACH B is similar in size to *Paedotherium minor*, but with striking dental similarities to *Pachyrukhos*. Compared to *Pachyrukhos*, though, PACH B has distinctly wide (labiolingually) and triangular P3-4 (these premolars are narrower and trapezoidal in *Pachyrkos*), and P4-M2 bear salient labial ridges separated by distinct grooves (some specimens of *Pachyrukhos* bear subtle labial grooves on the cheek teeth, but the ridges and grooves of PACH B are much more pronounced). The overall similarities between PACH B and *Pachyrukhos moyani* led us to consider assigning PACH B to a new species within *Pachyrukhos*, but we opted against this for several reasons: 1) the diagnostic dental characters of PACH B seem as robust as those diagnosing *Pachyrukhos*, *Tremacyllus*, and *Paedotherium*; 2) post-Oligocene pachyrukhines are also diagnosed by several skull characteristics that are not preserved in PACH B; 3) our phylogenetic results do not support a particularly close relationship between PACH B and *Pachyrukhos*; in the consensus tree PACH B, *Paedotherium*, *Tremacyllus*, and *Pachyrukhos* are grouped in a single polytomy (figs. 3.8, 3.9); 4) *Pachyrukhos* is overdue for taxonomic revision.

**Pachyrukhinae indeterminate**: Two specimens from LdL, both partial left skulls and mandibles in occlusion, cannot be precisely identified, but clearly have close affinities with the clade of late-Oligocene pachyrukhines (PACH B, *Pachyrukhos*, *Tremacyllus*,

*Paedotherium*). SGOPV 3970, recovered from Estero Campamento (figs. 3.1, 3.2), is potentially assignable to *Pachyrukhos moyani*, but a lack of preserved diagnostic morphology prevents firm taxonomic conclusions. SGOPV 5553, from Trapa Trapa East, potentially represents a new taxon, an abnormally small specimen of *Pachyrukhos*, an early occurrence of *Paedotherium* with an atypically large P2, or a specimen of PACH B that lacks salient labial ridges and grooves on P4-M2. Both SGOPV 3970 and SGOPV 5553 are excluded from the hypodigm of PACH B partly because they lack salient labial ridges on P4-M2, which we propose is diagnostic of this taxon (PACH B is also diagnosed by labiolingually wide P3-4; in SGOPV 3970 these teeth are not preserved and in SGOPV 5553 the width of these teeth are obscured by tight occlusion with the lower dentition). If additional fossil material suggests that PACH B is not consistently characterized by these distinct labial ridges, it would require a slight emendation to the diagnosis of this taxon and a reassessment of SGOPV 3970 and SGOPV 5553.

**Hegetotheriidae Phylogeny**: Combining datasets from previous analyses and incorporating the taxa described herein, this study advances our understanding of hegetotheriid evolution. Our results (along with those of Kramarz and Paz [2013]) underscore the need for a more inclusive phylogenetic definition of Hegetotheriidae. We propose that Hegetotheriidae be defined as the clade composed of all taxa more closely related to *Paedotherium bonaerense* than they are to Mesotheriidae, *Archaeotypotherium*, *Protarchaeohyrax*, or *Archaeohyrax*. Given this definition, the membership of Hegetotheriidae is consistent across all studies of hegetotheriid relationships (Cifelli, 1993; Cerdeño and Bond, 1998; Croft and Anaya, 2006; Billet *et al*., 2009; Billet, 2010; Reguero and Prevosti, 2010; Kramarz and Paz, 2013). A notable synapomorphy of Hegetotheriidae is hypselodont dentition, which presumably contributed to the Deseadan radiation of this clade.

Our results strongly support pachyrukhine monophyly, and we affirm the phylogenetic definition of Pachyrukhinae proposed by Reguero and Prevosti (2010, p. 156): "the MRCA of *Propachyrucos* and *Paedotherium* and all of its descendants." Our results do not resolve relationships among post-Oligocene pachyrukhines (PACH B, *Pachyrukhos*, *Tremacyllus*, *Paedotherium*). Considering these and other recent results (Cerdeño and Bond, 1998; Reguero and Prevosti, 2010), we suggest that future phylogenetic analyses may be improved by treating each species of *Tremacyllus* and *Paedotherium* as separate taxa. Although most previous studies resolve Deseadan pachyrukhines (*Propachyrukhos*, *Prosotherium*, *Medistylus*) as a clade (Cifelli, 1993; Cerdeño and Bond, 1998; Croft and Anaya, 2006; Reguero and Prevosti, 2010), in our tree these taxa appear as a paraphyletic assemblage at the base of Pachyrukhinae. This result suggests a sequential loss of dentition during pachyrukhine evolution: *Propachyrukhos* possessed at least vestigial I2-C/i3-c, but these teeth were progressively lost in *Medistylus* and *Prosotherium*, and then P1 was also eventually lost in all post-Oligocene taxa (PACH B, *Pachyrukhos*, *Tremacyllus*, *Paedotherium*).

In the present analysis "Hegetotheriinae" is paraphyletic (as in Croft and Anaya, 2006; Reguero and Prevosti, 2010). HEG A and *Hemihegetotherium* are resolved in a clade that is sister-group to Pachyrukhinae (consistent with Croft and Anaya, 2006); HEG A + *Hemihegetotherium* + Pachyrukhinae are united by two synapomorphies: m3 is trilobed and i1 is significantly larger than i2. Our results also suggest that neither *Prohegetotherium* nor *Hegetotherium* are monophyletic, highlighting the need for taxonomic revision of these genera, and providing direction and impetus for future studies seeking to elucidate hegetotheriid relationships.

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Appendix 3.1: Hegetotheriid taxa, references consulted, and specimens used for the phylogenetic analysis

- *Archaeotypotherium propheticus* (Ameghino, 1897): Croft *et al.*, 2003; Billet *et al.*, 2009
- *Protarchaeohyrax gracilis* (Roth, 1903): Reguero *et al.*, 2003; Billet *et al.*, 2009
- *Archaeohyrax patagonicus* Ameghino, 1897: Ameghino, 1897; Croft and Anaya, 2006; Billet *et al.*, 2009; MACN-A 52-617
- *Archaeohyrax suniensis* Billet *et al.*, 2009: Billet *et al.*, 2009
- *Hegetotheriopsis sulcatus* Kramarz, 2013: Kramarz, 2013
- *Sallatherium altiplanense* Reguero and Cerdeño, 2005: Reguero and Cerdeño, 2005; Croft and Anaya, 2006; Billet *et al.*, 2009
- *Prohegetotherium sculptum* Ameghino, 1897: Ameghino, 1897; Kramarz and Paz, 2009; MACN-A 52-443, MACN-A 52-444, MACN-A 52-448, MACN-A 52-449, MACN-A 52-550
- *Prohegetotherium schiaffinoi* (Kraglievich, 1932): Reguero and Cerdeño, 2005; Kramarz and Paz, 2009
- *Hegetotherium mirabile* Ameghino, 1887b: Ameghino, 1887b; Sinclair, 1909; McCoy and Norris, 2012; various specimens in MACN, MLP, and YPM-PU collections
- *Hegetotherium novum* Bordas, 1939: Bordas, 1939; MACN 11749
- *Hemihegetotherium achathaleptum* Rovereto, 1914: Rovereto, 1914; Cerdeño and Contreras, 2002, Cerdeño and Montalvo, 2002, Croft and Anaya, 2006
- *Hemihegetotherium torresi* (Cabrera and Kraglievich, 1931): Cabrera and Kraglievich, 1931; Croft and Anaya, 2006
- *Hemihegetotherium trilobus* Croft and Anaya 2006: Croft and Anaya 2006
- *Propachyrucos smithwoodwardi* Ameghino, 1897: Ameghino, 1897; Cerdeño and Bond, 1998; Croft and Anaya, 2006
- *Propachyrucos ameghinorum* Simpson, 1945b: Simpson, 1945b; AMNH 29574; Cerdeño and Bond, 1998; Croft and Anaya, 2006
- *Medistylus dorsatus* (Ameghino, 1903): Reguero *et al.*, 2007; Reguero and Prevosti, 2010
- *Prosotherium garzoni* Ameghino, 1897: Ameghino, 1897; Loomis, 1914; Cerdeño and Bond, 1998; Croft and Anaya, 2006
- *Pachyrukhos moyani* Ameghino, 1885: Ameghino, 1885, 1887a, 1889; Sinclair, 1909; various specimens in AMNH, MACN, MLP, and YPM-PU collections
- *Tremacyllus impressus* (Ameghino, 1888): Cerdeño and Bond, 1998; Croft and Anaya, 2006
- *Paedotherium minor* Cabrera, 1937: Cabrera, 1937; Cerdeño and Bond, 1998; Croft and Anaya, 2006
- *Paedotherium bonaerense* (Ameghino 1887c): Cerdeño and Bond, 1998; Croft and Anaya, 2006
- *Paedotherium typicum* (Ameghino, 1887c): Cerdeño and Bond, 1998; Croft and Anaya, 2006

Appendix 3.2: Characters and character states used in the phylogenetic analysis.

These represent a combination of characters from Croft and Anaya (2006) and Billet *et al.*, (2009). In turn, each of those studies incorporates characters from previous studies (consult those publications for further detail). After each character, and before the character states, the abbreviations in parentheses indicate the character number from Croft and Anaya (2006) (CA#) and/or Billet *et al.*, (BB#), and any changes to that character is also noted. The phylogenetic analysis of Billet et al. (2009) focused on the relationships of "archaeohyracids," mesotheriids, and hegeototheriids; consequently the following characters from that study were excluded from the present analysis, as they were uninformative for the taxa considered herein: 2, 3, 5, 7, 12, 15, 17, 18, 19, 29, 30, 32, 36, 37. All characters treated as unordered.

1. **Cementum** (CA1): (0) thin or absent; (1) thick.
2. **Crown height of cheekteeth** (modified from BB14, uninformative character state removed): (0) very hypsodont HI>1.75; (1) hypselodont, unknown HI.
3. **I2/i3**: (0) present or variably present; (1) absent.
4. **C/c**: (0) present or variably present; (1) absent.
   Characters 3 and 4 are adapted from character 2 in Croft and Anaya (2006), where they are treated as one character ("I2-C/i3-c: present [0]; absent [1]"). *Medistylus* possesses I2 but lacks the canine, which prompted us to score this as two separate characters.
5. **Relationship of canine and anterior premolars** (CA4, but a typographical error therein is corrected): (0) all lying directly in-line with rest of toothrow; (1) root of C labial to P1 and p1 labial to p2.
6. **P1/p1** (CA3): (0) present or variably present; (1) always absent.
7. **Relative size of I1** (CA5; similar to BB 1): (0) mesio-distal length <20% larger than that of M1; (1) mesio-distal length ≥ 20% than that of M1.
8. **Relative size of P2**. (CA6): (0) at least 80% length of P3; (1) less than 75% length of P3.
9. **Persistent, long, and flat lingual wall of upper molars** (BB6; similar to CA7): (0) absent; (1) present.
10. **Angle formed by ectoloph and distal face of M1** (CA8): (0) greater than 90 degrees; (1) approximately equal to 90; (2) less than 90.
    Croft and Anaya (2006) score this character as "0" for *Propachyrucos* and *Prosotherium*, but our own observations suggest these taxa should be scored as "1" for this character.
11. **General shape of upper M3 occlusal surface** (modified from CA10, uninformative character state removed): (0) rectangular or trapezoidal; (1) semicircular.
12. **Pronounced notch of posterior face of M3** (modified from CA11, polarity reversed and outgroup scored differently): (0) present; (1) absent.
13. **Reduced M3 (smaller than M2 in surface at all wear stages)** (BB4, similar to CA9): (0) absent; (1) present.
14. **i1 significantly larger than i2** (BB8; similar to CA12): (0) absent; (1) present.

15. **Flat and straight lingual face on lower molars at all stages of wear** (BB9, similar to CA13): (0) absent; (1) present.
16. **Constant, deep labial sulcus separating trigonid and talonid** (wording changed slightly from BB11): (0) absent; (1) present.
17. **m1-2 with regular shape throughout wear** (BB10): (0) absent; (1) present with rounded lobes labially and semi-circular trigonid; (2) present with lobes angulate labially.
18. **Labial sulcus on m3 talonid** (modified from BB13, character states 0 and 1 combined into state 0; similar to CA14): (0) absent or weak/inconsistent; (1) always well-marked; (2) very strong.
19. **Size of incisive foramina** (CA15; similar to BB16): (0) restricted to premaxilla; (1) extended beyond premaxilla.
20. **Triangular and forward pointing lacrymal** (BB20): (0) absent; (1) present.
21. **Strangled maxillary depassing the posteriormost extremity of nasals** (BB21): (0) absent; (1) present.
22. **Orbit** (wording slightly changed from BB22): (0) moderately enlarged; (1) greatly enlarged.
23. **Infraorbital foramen above molars** (modified from BB23, polarity reversed): (0) present; (1) absent.
24. **Zygomatic plate (in front of orbit)** (BB24): (0) absent; (1) present.
25. **Greatly reduced postorbital constriction** (BB25): (0) absent; (1) present.
26. **Temporal lines (forming the sagittal crest)** (BB26; similar to CA18): (0) fused temporal lines, sagittal crest well developed; (1) fusion of the temporal lines only in the most posterior part; (2) no fusion between the temporal lines.
27. **Hypertrophied epitympanic sinuses, prominent in dorsal view** (BB27; similar to CA19): (0) absent; (1) present.
28. **Crista meatus** (BB31): (0) well developed; (1) vestigial.
29. **Squamosal contact with frontal at the level of the post-orbital apophysis** (BB33): (0) absent; (1) present.
30. **Descending process of the maxillary developed as a spine laterally to the infra-orbital foramen** (BB34): (0) absent; (1) present.
31. **Numerous accessory foramina perforating the maxillary in front of the infra-orbital foramen** (BB35): (0) absent; (1) present.
32. **Configuration of the tibia and fibula** (CA20; BB38): (0) unfused; (1) short, broad distal fusion; (2) long, narrow distal fusion.
33. **Paroccipital apophysis and processus post-tympanic define a lamelliform extension on the postero-ventral part of the bulla** (BB39): (0) absent; (1) present.
34. **Post-incisive depressions** (CA16): (0) absent; (1) present.
35. **Post-oribtal process** (CA17): (0) well-pronounced, located anterior to posterior border of frontal; (1) little pronounced, located near or posterior to posterior to end of frontal
36. **Metapodial distal keel** (CA21): (0) incomplete; (1) complete.

Appendix 3.3: Character taxon matrix for Interatheriinae.

For polymorphic taxa, a letter is used to represent multiple states: 'A' indicates character states 0 and 1; 'B' indicates character states 1 and 2. "Outgroup" character states were coded by determining the ancestral characters of the clade (*Archaeotypotherium*, (*Protarchaeohyrax*, *Archaeohyrax*)), which was identified as the outgroup to Hegetotheriidae by Billet *et al*., (2009) and *Kramarz et al*., (2013). Most outgroup character states could be determined from the data matrix of Billet *et al*., (2009), but for several character states specimens and publications for outgroup taxa were consulted (see Appendix 3.1).

| | | | | | 5 | | | | | 10 | | | | | 15 | | | | | 20 | | | | | 25 | | | | | 30 | | | | 35 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| outgroup | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | ? |
| *Hegetotheriopsis* | 0 | 1 | 0 | 0 | ? | 0 | ? | ? | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | ? | ? | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? | 0 | 0 | ? | ? | ? | ? | ? |
| *Sallatherium* | ? | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | ? | ? | ? | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? | 0 | ? | ? | 0 | ? | ? |
| *Prohegetotherium sculptum* | ? | 1 | 0 | 0 | 1 | 0 | ? | 0 | 1 | 1 | ? | 0 | 1 | 0 | 1 | 1 | 1 | 0 | ? | ? | ? | ? | 0 | 1 | ? | ? | ? | ? | ? | ? | 0 | ? | ? | ? | ? | ? |
| *Prohegetotherium shiaffinoi* | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | ? | ? |
| *Hegetotherium mirabile* | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | B | A | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Hegetotherium novum* | ? | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | 0 | 1 | 1 | ? | ? | ? | ? | ? | 0 | ? | ? | 0 | 0 | 1 | 1 | ? | ? | ? | ? | 0 | 0 | ? | ? | ? | ? | ? |
| HEG A | ? | 1 | 0 | 0 | 1 | 0 | ? | 0 | 1 | 1 | 0 | 1 | 1 | ? | 1 | 1 | ? | 2 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Hemihegetotherium trilobus* | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | A | 1 | 1 | B | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | ? |
| *Hemihegetotherium* | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | B | 0 | ? | ? | ? | ? | ? | ? | ? | 1 | 0 | ? | ? | ? | ? | 1 | ? | 0 | ? | 0 |
| *Propachyrucos* | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 2 | ? | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| *Medistylus* | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | ? | ? | ? | ? | ? | 1 | ? | ? | 1 | 1 | 1 | 1 | 2 | 1 | ? | ? | ? | ? | ? | ? | 0 | ? | ? |
| *Prosotherium* | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| PACH B | ? | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | ? | ? | ? | ? | ? | 1 | ? | ? | ? | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Tremacyllus* | 0 | 1 | 1 | 1 | 0 | 1 | 1 | A | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 |
| *Pachyrukhos* | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 1 | 0 |
| *Paedotherium* | 0 | 1 | 1 | 1 | 0 | 1 | 1 | A | 1 | B | A | 1 | 0 | 1 | 1 | 1 | 2 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 1 | 1 |

Chapter 4. A consideration of taphonomic biases impacting the fossil mammal assemblages from the Laguna del Laja region

LIST OF FIGURES AND TABLES

# Chapter 4. A consideration of taphonomic biases impacting the fossil mammal assemblages from the Laguna del Laja region

## INTRODUCTION

The first significant collections of South American fossil mammals were recovered from Patagonian Argentina (e.g., Ameghino, 1887, 1889, 1894, 1895, 1897, 1902, 1906; Roth, 1898; Tournouër, 1903; Sinclair, 1909; Loomis 1914; Rovereto, 1914), and the this region continues to figure centrally in South American paleontology. Accordingly, much of our knowledge of mammal evolution in South America is based on the Patagonian fossil record (Marshall *et al.*, 1983; Pascual and Jaureguizar, 1990; Pascual *et al.*, 1996). The last three decades have witnessed a steady proliferation of important fossil localities outside of Patagonia, providing a more geographically complete understanding of mammalian evolution in South American (e.g., Wyss *et al.*, 1990, 1993, 1994; Muizon, 1991, 1998; Flynn *et al.*, 1995, 2002a, 2002b, 2003, 2008; Muizon *et al.*, 1997; Kay and Madden, 1997; Kay *et al.*, 1997; Muizon and Cifelli, 2000; Croft, 2001, 2007; Croft *et al.*, 2003a, 2003b, 2004, 2008; Croft and Anaya, 2006). While taxonomic differences between coeval faunal assemblages from geographically widespread regions are well documented, there have been very few attempts to examine the effects of taphonomic processes on the compositions of South American paleomammal faunas (but see Bown and Larriestra, 1990; Marshall *et al.*, 1995; Cladera *et al.*, 2004; Montalvo *et al.*, 2008). Recently collected fossil mammals from the Laguna del Laja (LdL) region, in the Andes of central Chile, provide a unique opportunity to consider the extent to which taphonomic biases, in particular those stemming from differential transport, may have impacted the fossil assemblage recovered from the LdL region.

Between 2001-05, several hundred fossil mammal specimens were recovered from a 100 $km^2$ region southeast of Laguna del Laja (LdL), in the Andes of Chile (~37.5º S, 71º W). These collections include well-preserved skulls, jaws, isolated teeth and postcranial skeletal elements, the vast majority of which are disarticulated (suggesting an accumulation of decaying skeletal elements, rather than the entrainment of living individuals [Behrensmeyer and Hook 1992]). Five geographically distinct, stratigraphically overlapping collecting areas have yielded mammalian fossils. (Herriott, 2006; Wertheim, 2007; Flynn *et al.*, 2008) (figs. 4.1). Most fossils derive from the Cura Mallín Formation (CMF), portions of which are well exposed at different locations throughout the region, together recording a ~1.9 km thick sedimentary sequence (fig. 4.2) (Herriot, 2006). An ~800 m sequence of the Trapa Trapa Formation (TTF) overlies the CMF east of Estero Trapa Trapa (figs. 4.1, 4.2); the lower member of the TTF (unit $Ttt_1$) has yielded three specimens. The exposed strata in the LdL region consist primarily of volcano-sedimentary units (fig. 4.2), interpreted as lahar flows deposited on intra-arc floodplains (Herriott, 2006; Flynn *et al.*, 2008). Fossils are most commonly recovered from coarse-grained, matrix supported sediments, suggesting *en masse* freezing (Herriot, 2006). These sedimentary features are consistent with high-energy hyperconcentrated flows and debris flows (Vallance, 2000; Herriot 2006).

In addition to the fossiliferious units, interbedded ash-fall tuffs and ignimbrites have yielded 17 high-precision $^{40}Ar/^{39}Ar$ dates throughout the sequence (Herriot, 2006), providing a stratigraphically consistent series of ages ranging from ~20-9 Ma (early to late Miocene) (fig. 4.2). Fossils have been recovered from across most of this interval, but a significant majority of specimens were collected from the lower units of the CMF, ranging in age from ~20-16 Ma (early Miocene) (fig. 4.2). This time span corresponds to the Colhuehuapian and Santacrucian South American Land Mammal Ages (SALMAs) (Marshall *et al.*, 1986; Flynn

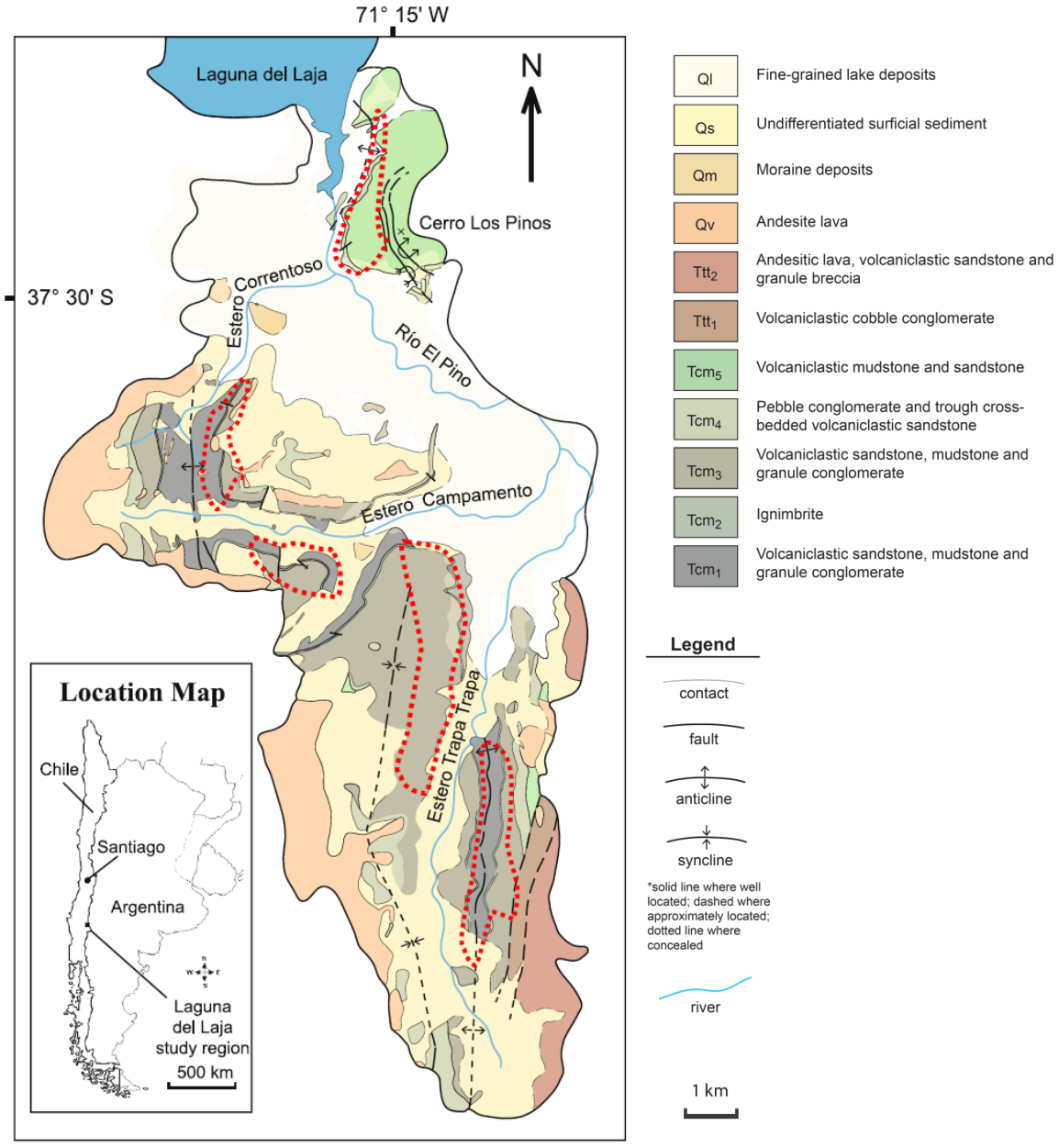


FIGURE 4.1. Map of the Laguna del Laja study area. Generalized geological map showing the sedmimentary units discussed in the text. Fossil mammal sampling subregions are encolosed by red, stippled lines. These collecting regions are infromally designated as (from north to south) Cerro Los Pinos, Estero Correntoso, Estero Campamento, Estero Trapa Trapa West, and Estero Trapa Trapa East. Inset shows the location of the study area within Chile. Modified from Flynn et al., 2008.

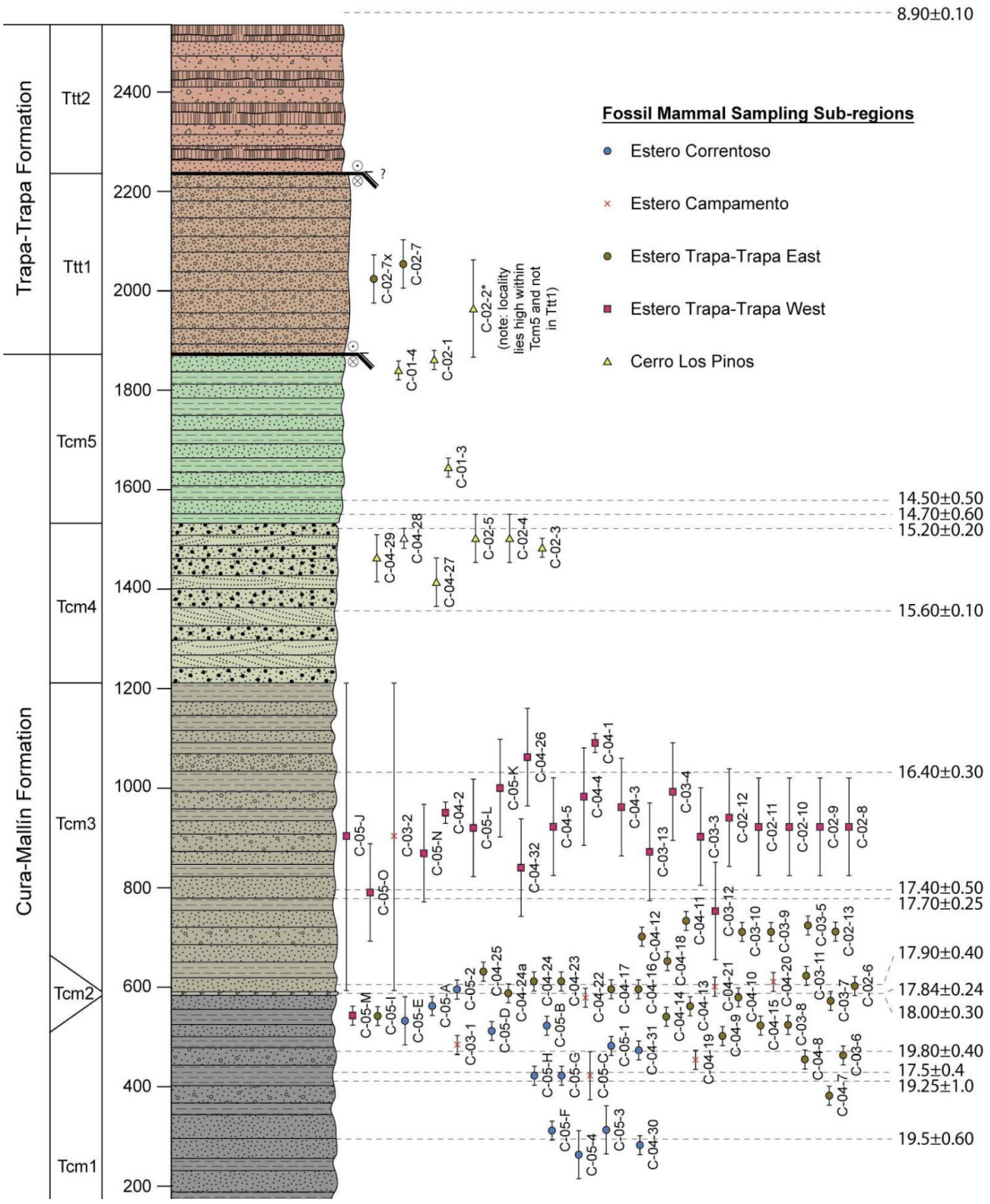


FIGURE 4.2. Stratigraphic section of the Cura Mallín and Trapa Trapa formations in the region southeast of Laguna del Laja. This is a composite stratigraphy based on correlation from a number of different locations, since the sequence is nowhere exposed in its entirety at one site. Stratigraphic positions of fossil localities are shown. The vertical height of "error bars" associated with each locality represent the level of uncertainty in stratigraphic position, with short bars indicating well-constrained stratigraphic positions and longer bars indicating moderately to poorly constrained stratigraphic positions. $^{40}Ar/^{39}Ar$ dates are also indicated. See fig. 1.6 for stratigraphic column legened. Figure from Herriot (2006).

and Swisher, 1995; Fleagle *et al.*, 1995; Wertheim, 2007; Re *et. al*, 2010; Perkins *et al.*, 2012; Dunn *et al*., 2013) (fig. 4.3b). The "type" localities of these SALMAs, and other localities discussed in this study, are shown in fig. 4.3a.

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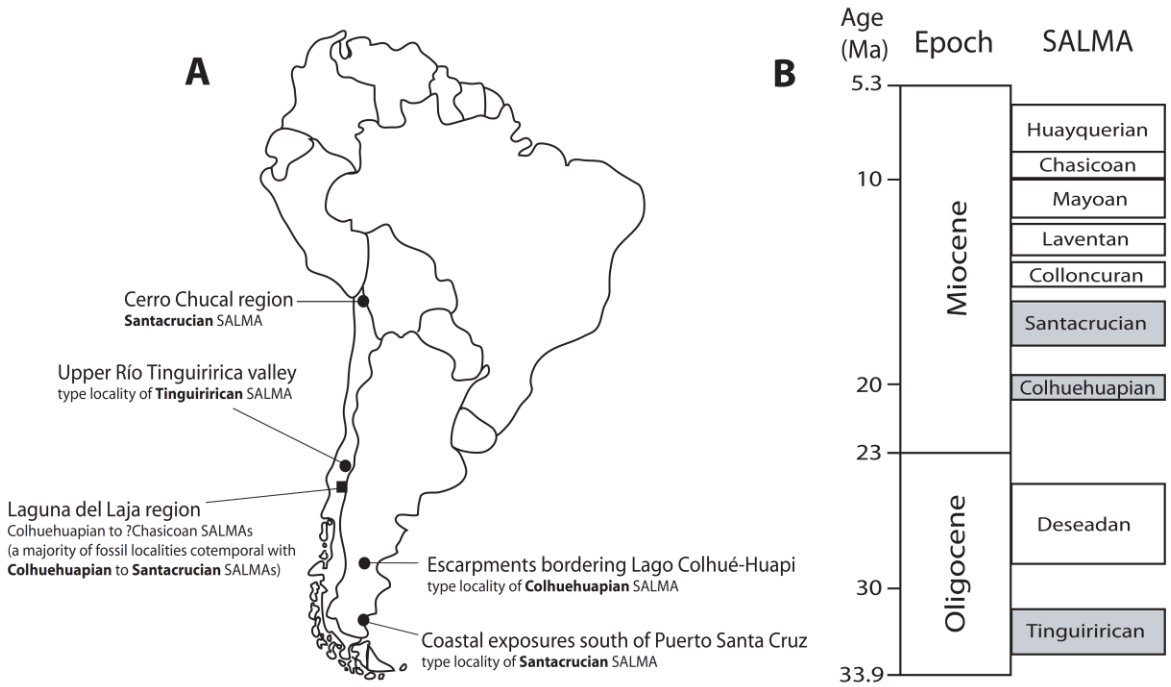


FIGURE 4.3. Fossil localities and South American Land Mammal "Ages" (SALMAs). **A**: Map of South America showing the primary fossil localities discussed in the text. **B**: Geologic time scale of Oligocene and Miocene, highlighting (in grey) SALMAs discussed in the text.

The first detailed studies of LdL fossils indicated a high level of taxonomic novelty. Wertheim's (2007) taxonomic analysis of the rodents from LdL treated 26 specimens assigned to 22 taxa, of which 20 represented new species (including 10 new genera). Shockey *et al.* (2012) assigned a well-preserved upper left dentition from LdL to *Colpodon antucoensis*, a new species of leontiniid (Toxodontia, Notoungulata). Fourteen specimens of typotherian notoungulate specimens at LdL have been identified at the species-level; these are referred to six taxa, five of which represent new genera (Chs. 2-3). Wertheim (2007) hypothesized that this high degree of endemism could be related to geographic isolation and habitat fragmentation caused by local uplift of the Andean Main Range.

Taxa of small and medium body size constitute a significant proportion of the fossils recovered from the LdL region. Typotherian notoungulates and caviomorph rodents are especially common; even the largest representatives of these groups at LdL, such as *Protypotherium*, likely had body masses of less than 10 kg (Croft and Anderson, 2008; Cassini *et al.*, 2012a, 2012b). Not only is the abundance of small, endemic taxa surprising, but also unexpected is the absence of large bodied species (i.e., with body masses greater than 10 kg) common in many coeval faunas from elsewhere in South America. Moreover, it is evident that fossils from LdL consist overwhelmingly of teeth and cranial elements. Significant numbers of teeth and cranial elements are a common feature of paleo-mammal collections (e.g., Bown and Larriesta, 1990; Flynn *et al.*, 2003; Cladera *et al*., 2004; Croft, 2007; Montalvo *et al.*, 2008; personal obs.), which can be partly attributed to the high enamel content of teeth and relatively high mineral density of cranial bones (Lyman, 1982, 1984), making these skeletal elements more resistant to destruction (Lyman, 1982; Klein and Cruz-Uribe, 1984) (collecting biases also play a role; see discussion below). Nevertheless, the staggering prevalence of teeth and cranial elements at LdL merits further consideration,

especially as several influential taphonomic studies suggest that skewed "bone groups" in paleontological and archeological collections reflect variable susceptibility to hydrodynamic transport (Voorhies, 1969; Behrensmeyer, 1975, 1982; Dodson, 1973; Boaz and Behrensmeyer, 1976; Hanson, 1980). Collectively, these studies indicate that denser bones, like mandibles and cranial elements, are less susceptible to fluvial transport, and are thus often associated with lag deposits (accumulating close to where transport begins) in high-energy fluvial environments, as more transportable elements (e.g., ribs and vertebra) are carried further downstream.

Beyond preliminary impressions, no quantitative analysis focusing on size and skeletal element composition of LdL fossils has been carried out, and detailed comparisons of these parameters are not available from other locations. This study addresses the potential influence of depositional processes on the fossil assemblages at LdL. Data presented herein are consistent with the conclusion that the depositional environments at LdL may help to account for unexpected dearth of large mammals and prevalence of dental and cranial elements.

## MATERIALS AND METHODS

The primary focus of this study is to determine how local depositional settings may have influenced faunal characteristics at LdL, especially with regard to the predominance of small bodied taxa and dental/cranial elements. To quantify the size distribution of representative taxa, the number of identified specimens per taxon (NISP) at LdL is recorded (figs. 4.4, 4.5). NISP was selected as our metric rather than minimum number of individuals

(MNI), because the focus here is to quantify the bias towards preservation of *specimens* of small-bodied taxa, not the number of individuals necessary to account for those specimens (for discussion of NISP and MNI, see Lyman, 1994). Family-level identifications are used because they are available for the majority of the specimens at LdL, while significantly fewer specimens have been identified to genus or species-level. Moreover, many families exhibit a narrow range of body sizes, such that the size of the specimen could be determined with reasonable confidence from its familial identification. Estimates of body masses for families were obtained from published sources (Fariña *et al.*, 1998; Croft, 2001; Flynn *et al.*, 2003; Elissamburu, 2004, 2011; Vizcaíno *et al.*, 2010; Scarrano *et al.*, 2011; Bargo *et al*., 2012; Candela *et al*., 2012; Cassini *et al.*, 2012a, 2012b; Kay *et al.*, 2012; Morgan and Álvarez, 2013). Body masses were binned into four classes: Size Class I: less than 1 kg; Size Class II: between 1-10 kg; Size Class III: between 10-100 kg; Size Class IV: greater than 100 kg. The NISP are shown both per family and per size class (figs. 4.4, 4.5). Size Classes I/II and Size Classes III/IV were combined in the tally of specimens per size class (fig. 4.5), since several families exhibit a range of body masses below 10 kg (e.g., Chinchillidae, and Hegetotheriidae include Size Class I and II taxa) or above 10 kg (e.g., Mesotheriidae and Homalodotheriidae include Size Class I and II taxa). Only specimens assigned to taxa with estimated body masses (Wyss *et al*., 1994; Flynn *et al*., 2003) are included in the tally (fig. 4.5).

"Bone groups" vary in their susceptibility to hydrodynamic transport, such that the relative abundance of different skeletal elements can be used to infer depositional environments and current velocities (Voorhies, 1969; Behrensmeyer, 1975, 1982). To quantify the distribution of bone types at LdL, I calculated the minimum number of individuals (MNI) per skeletal component (sensu Lyman, 1994) for mandibles, maxilla,

complete and partial skulls, isolated teeth, osteoderms, and postcranial elements (fig. 4.6, 4.7). The MNI for each skeletal portion was determined using various lines of evidence, including stratigraphic position (if two specimens were recovered from non-overlapping strata, they were assumed to belong to different individuals) and taxonomic considerations (specimens pertaining to different taxa clearly represent different individuals). Only fossils identified to the family-level were included in this analysis, as more detailed skeletal component information is available for these specimens.

These qualitative and quantitative features of the relative abundance of fossils at LdL are instructive in their own right, but they are more fully understood in comparison to other fossil assemblages. As mentioned above, most fossils from the LdL have been recovered from stratigraphic levels temporally coincident with the Colhuehuapian and Santacrucian SALMAs (fig. 4.2, 4.3b). Accordingly, faunal data from LdL are compared to fossil assemblages from well-known Colhuehuapian and Santacrucian localities (fig. 4.3a). Detailed specimen data are not available from the "type" localities of the Colhuehuapian and Santacrucian SALMAs, thus precluding rigorous comparison with the LdL specimen counts discussed above (i.e., NISP and MNI). Comparisons between the LdL assemblage and these "type" localities of the Colhuehuapian (escarpments bordering Lago Colhué-Huapi, in Argentine Patagonia) and Santacrucian (exposures of the Santa Cruz Formation south of Puerto Santa Cruz, in Argentine Patagonia) are thus limited to more generalized taxonomic, depositional, and paleoenvironmental observations available from published studies.

Detailed specimen data, which could be directly compared to LdL specimen counts, were available from two well-studied localities in Chile: the Cerro Chucal region, a Santacrucian locality from the Altiplano of northern Chile (Flynn *et al*., 2002; Croft *et al*., 2004; Croft *et al*., 2007), and the upper Río Tinguiririca valley, the "type" locality of the

Tinguiririca SALMA (early Oligocene), located in the Andes of central Chile (~300 km north of LdL) (Wyss *et al*., 1990, 1993, 1994; Flynn *et al*., 2003; Croft *et al*., 2008). Although the fossils from this location are early Oligocene in age (and thus more than ~10 Ma older than the earliest exposures at LdL), they are appropriate for comparison to LdL fossil size and skeletal type, because the fossil-bearing sediments at LdL and Tinguiririca have both been interpreted as volcaniclastic lahar deposits (Wyss *et al*., 1994; Charrier *et al*., 1996; Herriot, 2006). Data from Chucal and Tinguiririca are analyzed with the same methodology described above for the LdL fossils. Thus, NISP per family and size class (figs. 4.8-9 for Chucal; figs. 4.12-13 for Tinguiririca), and MNI per skeletal element (figs. 4.10-11 for Chucal; figs. 4.14-15 Tinguiririca) are compared from LdL, Chucal, and Tinguiririca. The notohippids (Notohippidae, Notoungulata) common at Tinguiririca include taxa with body masses ranging from ~5-23 kg (Size Classes II and III); two taxa have estimated body masses less than 10 kg ("*Eomorphippus* undescribed sp., near E. *obscurus*"; "'Rhynchippinae' undescribed taxon A"; Flynn *et. al*, 2003) and two taxa have estimated body masses greater than 10 kg ("'*Eomorphippus*' sp., cf. *pascuali*"; "'Rhynchippinae' undescribed taxon B"; Flynn *et. al*, 2003. Accordingly, only specimens assigned to taxa with estimated body masses (Wyss *et al*., 1994; Flynn *et al*., 2003) are included in the tally (fig. 4.5).

# RESULTS

*Taxa and body size distribution*

An exhaustive taxonomic comparison between the fossil faunas at these locations is beyond the scope of this study, but a few taxonomic features, especially with respect to size, are worth consideration. The fossil mammal faunas at LdL exhibit a high degree of taxonomic novelty, and large-bodied taxa are scarce. The most commonly recovered specimens from LdL included typotherian notoungulates (Hegetotheriidae and Interatheriidae, Size Classes I and II) and rodents (most commonly Chinchillidae and Echimyidae, Size Classes I and II, but also Agoutidae, and Eocardidae, Size Class II) (fig. 4.5). In fact, ~92% of specimens identified to family-level (80 out of 87) at LdL pertain to taxa with body masses less than 10 kg (Size Classes I/II); only seven specimens (~8%) pertain to taxa with body masses greater than 10 kg (Size Classes III/IV) (fig. 4.5).

Large mammals make up a significant proportion of Santacrucian and Colhuehuapian localities in Patagonia. At the "type" localities north and south of Lago Colhué-Huapi, in Argentine Patagonia (including the extensive exposures of the Gran Barranca) (fig. 4.3a), the Colhuehuapian fauna includes at least seven families and 13 genera with body masses greater than 100 kg (Marshall *et al.*, 1983). The Santacrucian SALMA, initially recognized from the richly fossiliferous, coastal exposures of the Santa Cruz Formation near Puerto Santa Cruz, in southern Argentine Patagonia, has long been noted for its large bodied mammals (e.g., Darwin, 1846; Ameghino, 1889; Scott, 1912, 1937). A recent paleoecological study of four Santacrucian localities along ~15 km of coastline (~75 km south of Puerto Santa Cruz), focusing on Fossiliferous Levels 1-7 of the Santa Cruz Formation (out of 10 such levels total), identified four families and seven genera with body

masses greater than 100 kg; out of 49 taxa reported in this region, 26 have body masses greater than 10 kg (Kay *et al*., 2012). Moreover, Santacrucian fossil collections are characterized not only by a diversity of large-bodied taxa, but also by high specimen abundances for some of these large mammals (e.g., Glyptodontidae and Toxodontidae; Vizcaíno *et al*., 2012; Cassini *et al*., 2012b; personal obs.).

Compared to the fauna from LdL, the assemblage at Chucal exhibits a significantly more uniform size distribution; in fact, the number of Size Class III/IV specimens outnumber Size Class I/II specimens (figs. 4.8, 4.9). One unique aspect of the Chucal fauna is the abundance of mesotheriid notoungulates (Mesotheriidae, Size Class III/IV; fig. 4.8) (Croft *et al*., 2004), which are almost completely unknown from typical Santacrucian localities (Marshall *et al.*, 1983).

As with fossils from LdL, the NISP of the Tinguiririca fauna is similarly skewed towards small-bodied taxa (Size Classes I/II) (figs. 4.13-14). This fauna is dominated by Interatheriidae and Archaeohyracidae (Size Classes I/II); Notohippidae is also well represented (Size Class II/III) (fig. 4.13). Only ~12% of specimens (20 out of 173) from Tinguiririca pertain to taxa larger than 10 kg (Size Class III/IV; fig. 4.14). At LdL, by comparison, the proportion of Size Class III/IV individuals is ~8%.

*MNI per skeletal element*

MNI per skeletal element could only be calculated for fossils collected from LdL (figs. 4.6, 4.7), Chucal (figs. 4.10. 4.11), and Tinguiririca (figs. 4.14, 4.15). Here again, the data from LdL and Tinguiririca are very similar. At both these locations, mandibles are the most overrepresented skeletal element (figs. 4.6, 4.14), and cranial elements (including teeth) comprise the vast majority of specimens (figs. 4.7, 4.15). At LdL, cranial elements

account for 89% of the MNI per skeletal portion, while at Tinguiririca this proportion is 88%. At Chucal, although cranial elements are still the most represented specimens (fig. 4.11), postcranial elements are much more common (and, grouped together, more abundant than any single cranial element) (fig. 4.10). At Chucal, cranial elements accounted for 63% of the MNI per skeletal portion. While this index is significantly lower at Chucal than at LdL or Tinguiririca, it is noteworthy that even at Chucal, cranial elements are certainly overrepresented with respect to postcranial elements.

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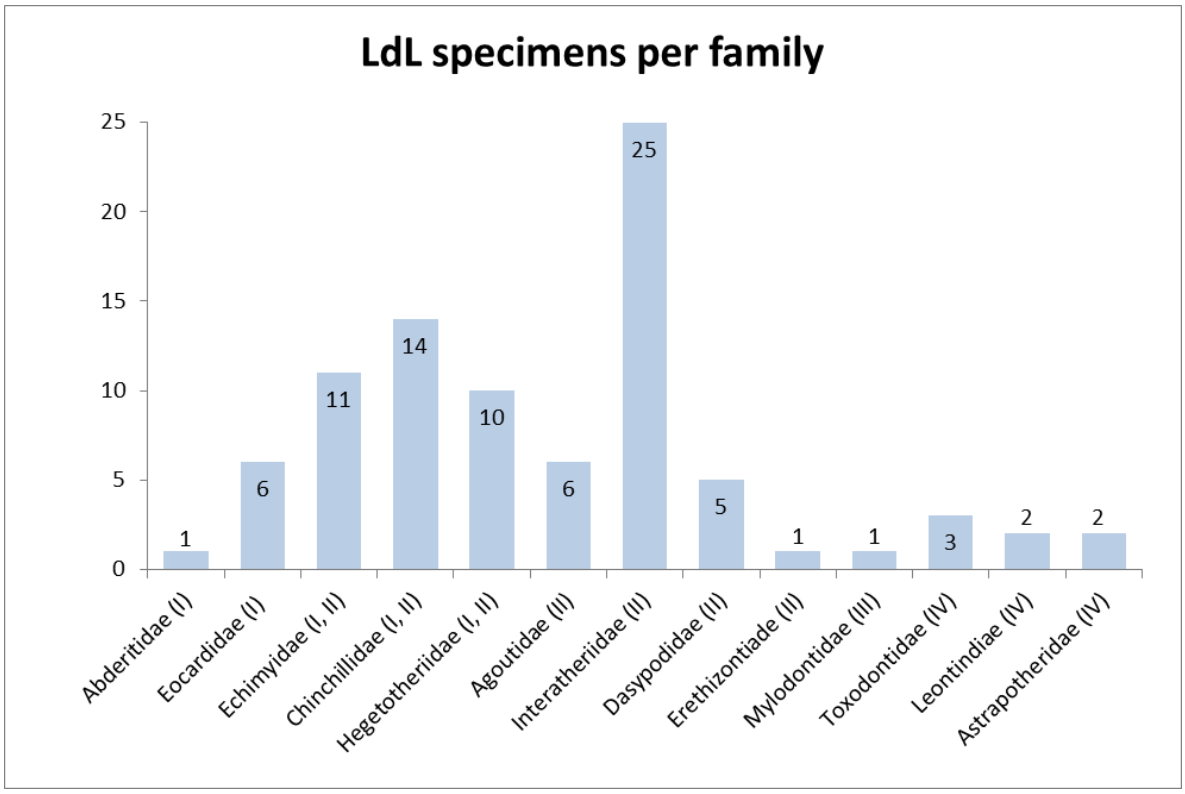


FIGURE 4.4. Specimens (NISP) per family at LdL. Size class of the family is in parenthesis after the family name. In some cases, a single family has representatives that belong to more than one size class. Size classes: I: less than 1 kg; II: 1-10 kg; III: 10-100 kg; IV: greater than 100 kg

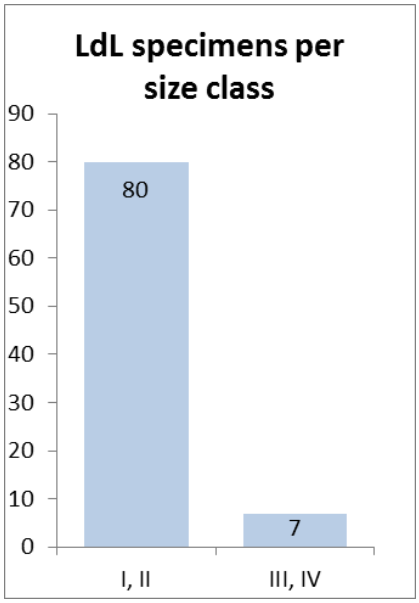


FIGURE 4.5. Specimens (NISP) per size class at LdL. Size classes: I, II: less than 10 kg; III, IV: greater than 10 kg.

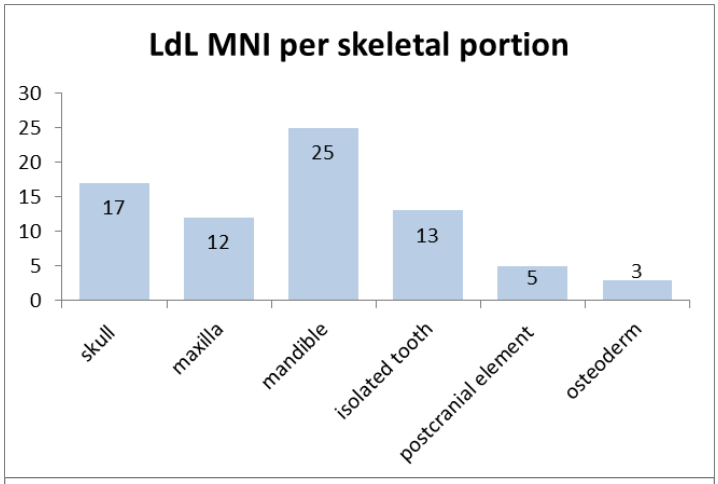


FIGURE 4.6. MNI per skeletal portion at LdL. "Skull" refers to elements that were identified as either partial or complete skulls, and counted separately from elements that were identified as partial or complete maxilla.

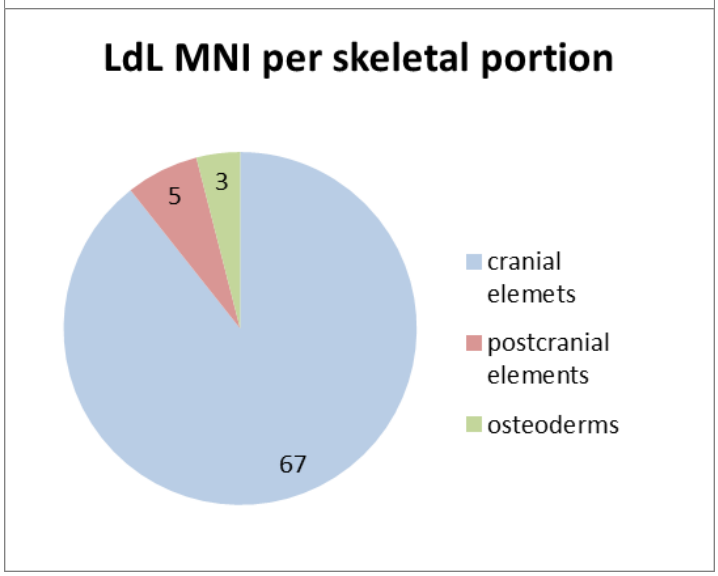


FIGURE 4.7. MNI per skeletal portion at LdL, summarized into three classes.

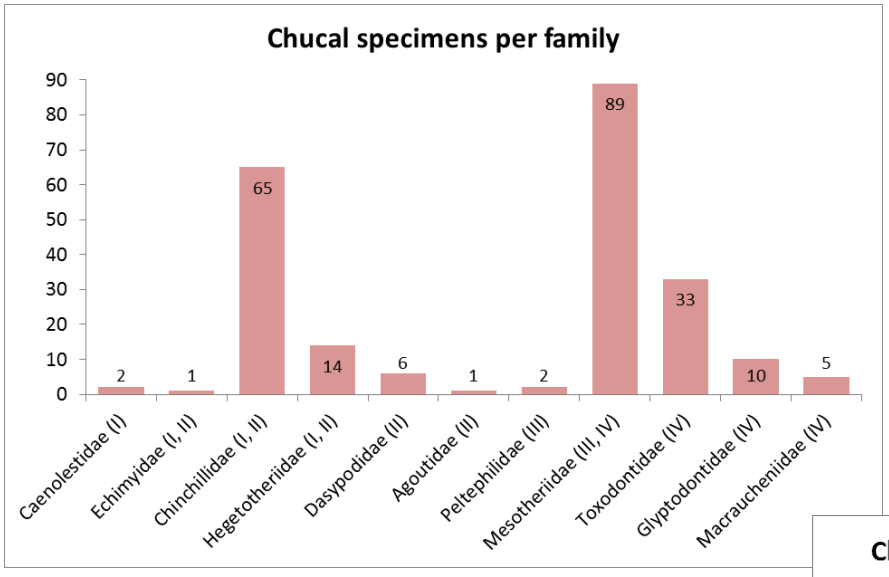


FIGURE 4.8. Specimens (NISP) per family at Chucal. Size class of the family is in parenthesis after the family name. In some cases, a single family has representatives that belong to more than one size class. Size classes: I: less than 1 kg; II: 1-10 kg; III: 10-100 kg; IV: greater than 100 kg.

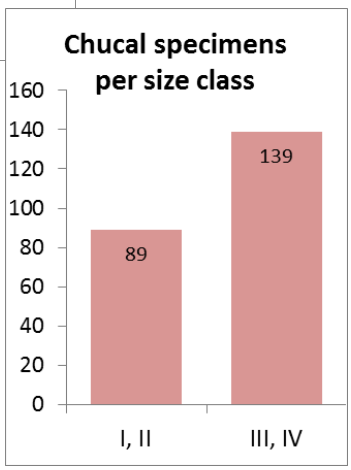


FIGURE 4.9. Specimens (NISP) per size class at Chucal. Size classes: I, II: less than 10 kg; III, IV: greater than 10 kg.

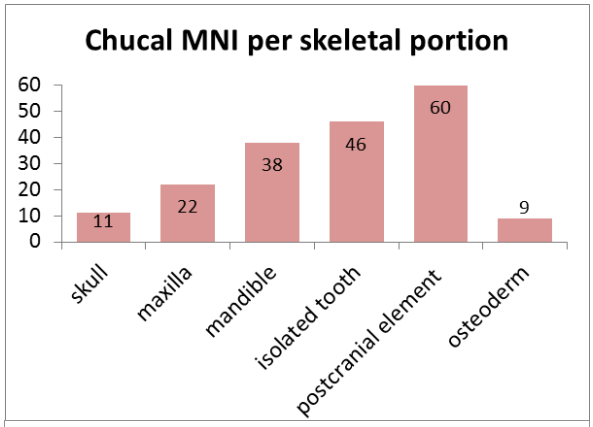


FIGURE 4.10. MNI per skeletal portion at Chucal. "Skull" refers to elements that were identified as either partial or complete skulls, and counted separately from elements that were identified as partial or complete maxilla.

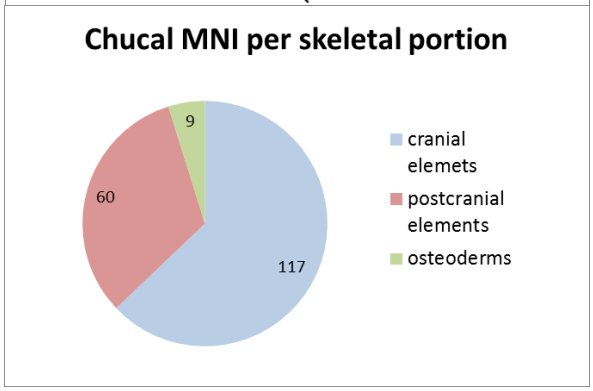


FIGURE 4.11. MNI per skeletal portion at Chucal, summarized into three classes.

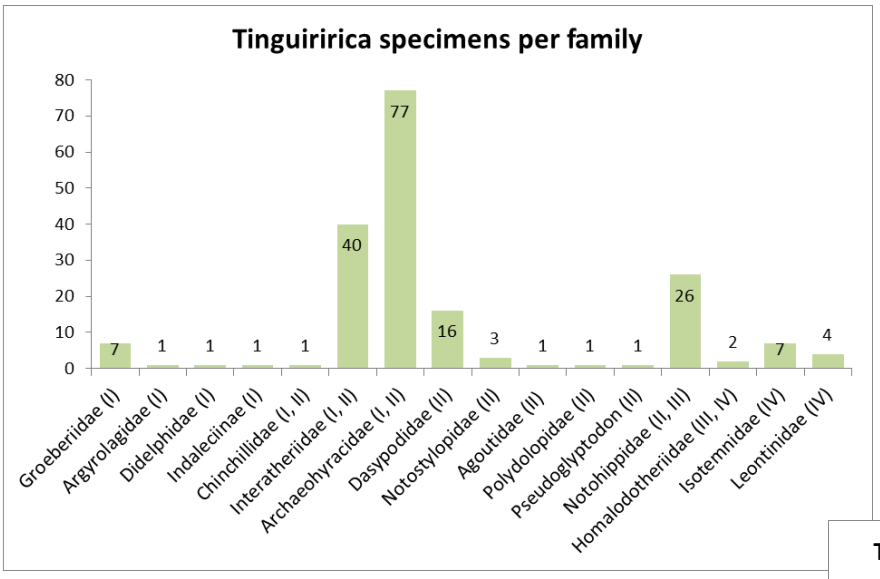


FIGURE 4.12. Specimens (NISP) per family at Tinguiririca. Size class of the family is in parenthesis after the family name. In some cases, a single family has representatives that belong to more than one size class. Size classes: I: less than 1 kg; II: 1-10 kg; III: 10-100 kg; IV: greater than 100 kg

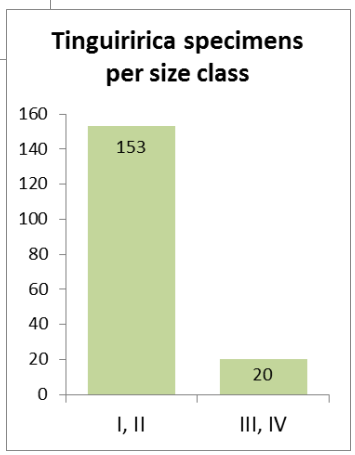


FIGURE 4.13. Specimens (NISP) per size class at Tinguiririca. Size classes: I, II: less than 10 kg; III, IV: greater than 10 kg.

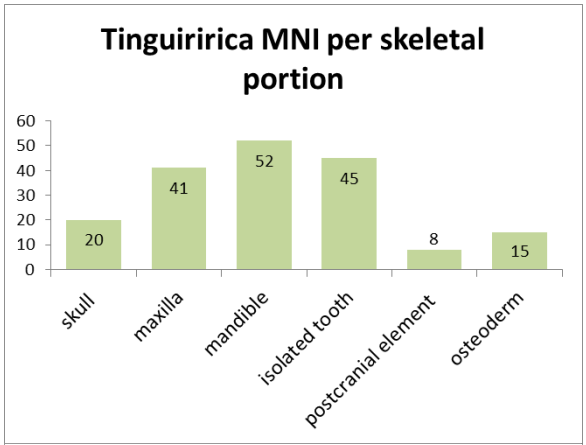


FIGURE 4.14. MNI per skeletal portion at Tinguiririca. "Skull" refers to elements that were identified as either partial or complete skulls, and counted separately from elements that were identified as partial or complete maxilla.

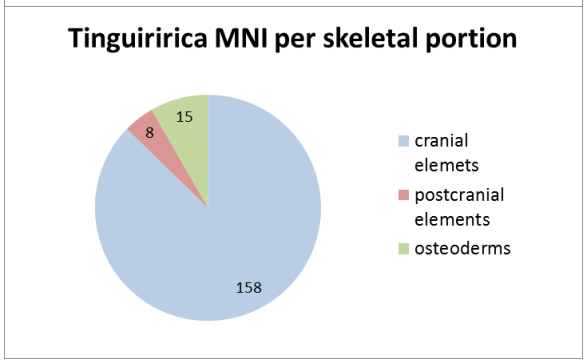


FIGURE 4.15. MNI per skeletal portion at Tinguiririca, summarized into three classes.

## DISCUSSION

The results of this study are summarized in table 4.1. Though temporally separated by at least ~10 Ma, the fossil assemblages at LdL and Tinguiririca are similar in being overwhelmingly composed of cranial elements of small-bodied taxa (Size Classes I/II). At Chucal, a Santacrucian locality in the Altiplano of northern Chile, cranial elements, while abundant, are not as highly represented as at Tinguiririca and LdL, and there is a much greater proportion of medium and large-sized taxa. The "type" Santacrucian and Colhuephuapian faunas, which are temporally coincident with most the most fossiliferous strata at LdL, are characterized by an abundance of well-represented medium and large-sized taxa (Ameghino, 1889, 1906; Scott, 1932, 1937; Marshall *et al.* 1983; Cassini *et al*., 2012b; Kay *et al*., 2012; Vizcaíno *et al*, 2012). Accordingly, the scarcity of large-sized taxa at LdL is striking. The similarities between LdL and Tinguiririca fossil assemblages may be due, in part, to their unique depositional settings.

**TABLE 4.1. Summary of results and comparisons between five localities.**
CE%: the proportion of the fossil assemblage composed of cranial elements (including teeth), based on MNI per skeletal portion. See text for references.

| Locality | SALMA (epoch) | Depositional Setting | Taxa/Size observations | CE% |
|---|---|---|---|---|
| Laguna del Laja region | Colhuehuapian to ?Chasicoan Most fossil localities cotemporal with Colhuehuapian to Santacrucian (early to late early Miocene) | volcaniclastic lahars in an intramontane basin | ~8% of specimens (7 out of 87) pertain to taxa larger than 10 kg | 89 (n=75) |
| Upper Río Tinguiririca valley | Tinguirirican (early Oligocene) | volcaniclastic lahars in an intramontane basin | ~12% of specimens (20 out 173) pertain to taxa larger than 10 kg | 88 (n=181) |
| Cerro Chucal region | Santacrucian (late early Miocene) | floodplain, fluviatile, and lacustrine facies | ~61% of specimens (139 out of 228) pertain to taxa larger than 10 kg | 63 (n=186) |
| Bordering Lago Colhué-Huapi | Colhuehuapian (early Miocene) | intraformational sandstones and conglomerates in bedload fluvial system | at least 7 families and 13 genera larger than 100 kg | NA |
| South of Puerto Santa Cruz | Santacrucian (late early Miocene) | mudstones, sandstones, tuffs in low-energy fluvial system | out of 49 taxa reported, 26 have body masses greater than 10 kg* | NA |

* based on a paleocological study of Fossiliferous Levels 1-7 (out of 10) of the Santa Cruz Formation at four coastal localities south of Puerto Santa Cruz (Kay *et al*., 2012).

*Skeletal element biases and depositional settings*

Cranial and dental elements commonly dominate collections of fossil mammals (e.g., Bown and Larriesta, 1990; Cladera *et al*., 2004; Montalvo *et al.*, 2008). This bias has several potential explanations: 1) collection bias: cranial and dental elements are often the most informative and diagnostic parts of the skeleton. As a result, these specimens are favored during collection and often given higher priority for fossil preparation and study; 2) differential survivorship: the enamel covering of teeth and high mineral density of cranial bones contribute to their greater resistance to destruction than post-cranial elements (Lyman, 1982, 1984; Klein and Cruz-Uribe, 1984); 3) differential transport and deposition: dense skeletal elements (e.g. teeth, mandibles, skulls), are less susceptible to fluvial transport, and are often associated with lag deposits in high-energy fluvial environments, as more transportable elements are carried further downstream (Voorhies, 1969; Behrensmeyer, 1975, 1982; Dodson, 1973; Boaz and Behrensmeyer, 1976; Behrensmeyer and Boaz; 1980; Hodson, 1980). These explanations are not mutually exclusive, and all three processes likely contribute to an overrepresentation of teeth and cranial elements. The same core group of researchers amassed fossils from LdL, Tinguiririca, and Chucal, suggesting that collection bias does not account for *differences* in the skeletal element proportions between these three localities. Collections from LdL, Tinguiririca, and Chucal all contain a majority proportion of cranial elements (≥63%) (table 4.1; figs. 4.6-7, 4.10-11, 4.14-15), but this percentage is much higher at LdL(89%) and Tinguiririca (88%) (figs. 4.6-7, 4.14-15).

At LdL and Tinguiririca, fossils occur in volcaniclastic sediments interpreted as lahar deposits which accumulated in intramontane basins (Wyss *et al.*, 1994; Charrier *et al.* 1996; Herriot, 2006). The predominance of skull and mandible elements (Voorhies Group III) at

LdL and Tinguiririca are consistent with lag deposition in a high-energy environment (Voorhies, 1969; Behrensmeyer, 1975, 1982; Dodson, 1973; Boaz and Behrensmeyer, 1976; Behrensmeyer and Boaz; 1980; Hanson, 1980). The specific effects of lahars on skeletal element sorting remain unstudied, but flows exhibiting high sediment and debris loads that settle *en masse* can certainly be considered high-energy environments (Herriot, 2006; Vallance, 2000), such that the effects of transport-mediated sorting are to be expected. Lahars become more dilute further downstream, ultimately leading to stream flood-flows (with low suspended sediment loads) at their furthest reaches (Smith and Lowe, 1991). In this context, the debris flow and hyperconcentrated flow deposits associated with lahars, from which LdL fossils have been recovered, are potentially analogous to the fluvial lag deposits in which high-density skeletal elements are preferentially recovered. In addition to transport sorting, differential survivorship of fossil material would also likely be more pronounced in these high-energy, debris-rich flows, resulting in the preferential preservation of the most durable skeletal remains, such as skulls, mandibles, and teeth (Lyman, 1982, 1984; Klein and Cruz-Uribe, 1984). Indeed, many strata LdL contain lithic fragments larger than some of the teeth they entomb; that fossils are preserved in such deposits is remarkable (and further suggest short transport distances). While cranial elements are still disproportionately represented at Chucal, specimens from this site did include a far greater proportion of postcranial elements. This may be explained by lower-energy depositional settings at Chucal, where fossils occur primarily in siltstones and sandstones with floodplain, fluviatile, and lacustrine facies (Croft *et al.*, 2004; Charrier *et al*., 2005). These relatively low-energy river and lake deposits would have resulted in less transport and survivorship sorting, compared to the high-energy depositional settings at LdL and Tinguiririca.

*Taxon size biases and depositional settings*

The predominance of small and medium-sized taxa at LdL (table 4.1; figs. 4.4, 4.5) is a striking feature. Coeval Colhuehuapian assemblages from Lago Colhué-Huapi, Argentina, as well as Santacrucian faunas from south of Puerto Santa Cruz, Argentina, and Chucal, Chile, are characterized by a diversity and/or abundance of large mammals (Ameghino 1902, 1906; Scott, 1932, 1937; Marshall *et al.* 1983; Croft *et al.*, 2004; Kay *et al*., 2012; Vizcaíno *et al*., 2012; Cassini *et al*., 2012b) (see table 4.1). The faunal assemblage from Tinguiririca, which is similar to the LdL faunal assemblage in terms of its geographic setting (central Chilean Andes) and depositional environment (volcaniclastic lahars), also exhibits an unusual dearth of large mammals (table 4.1; figs. 4.6, 4.7).

As discussed above, collection bias, differential survivorship, and differential transport may contribute to the predominance of cranial elements at LdL and Tinguiririca (and to a lesser extent, Chucal). The overrepresentation of *small-bodied taxa* at LdL and Tinguiririca, however, cannot be attributed to collection biases or differential bone survivorship. Large fossils tend to be more conspicuous during prospecting than small fossils; it is likely that a "size-dependent collection bias" would actually *favor* large-bodied taxa. Similarly, differential survivorship of skeletal elements likely cannot account for the observed scarcity of large mammals, since skeletal remains of large-bodied taxa often resist disarticulation, fragmentation, and destruction to a greater extent than those of smaller taxa (Dodson, 1973; Behrensmeyer, 1979, 1981; Retallack 1988).

The data presented here indicate that the high-energy depositional settings at LdL and Tinguiririca may have contributed to the predominance of dental and cranial elements represented in these faunas, since dense skeletal elements are less susceptible to fluvial transport. Similar density-dependent transport biases may also help explain the prevalence of

specimens pertaining to small-bodied taxa. Lyman *et al.* (1992) reported that the bones of marmots are denser than their counterparts in deer. If this pattern applies to small and large mammals generally (as suggested by Lyman, 1994), then high-energy lag deposits with pronounced transport sorting may preferentially preserve the denser elements of small taxa. Additionally, actualistic experiments indicate that the skeletons of small vertebrates become disarticulated more easily and quickly than their larger bodied kin, likely due the strength of the tendons that hold skeletons together (Dodson, 1973; Brand *et al*., 2003), and that articulated skeletons are transported more readily than individual elements (Coard and Dennel, 1995). Very few articulated fossils have been recovered from LdL or Tinguiririca[4]. Perhaps, then, the prevalence of disarticulated specimens of small taxa at LdL and Tinguirirca can be at least partly attributed to differential transport. Under this scenario, the denser and more easily disarticulated skeletal elements of smaller taxa are more likely to have settled quickly (deposited along with laharic debris and hyperconcentrated flows), whereas remains of larger taxa would have been carried further downstream. Being transported further, large skeletal elements are more likely to have been destroyed or deposited in settings that have not been sampled.

The proposed relationship between specimen size and depositional setting is consistent with the observation that the high-energy deposits at LdL and Tinguiririca preserve a significantly higher proportion of small-bodied taxa than the lower-energy deposits at Chucal (see table 4.1). Faunas from "type" Colhuehuapian and Santacrucian

[4] A tangential taphonomic note: Behrensmeyer and Hook (1992) suggest that mudflows may often preserve articulated skeletons, since these catastrophic events can trap living vertebrate fauna. Accordingly, the prevalence of disarticulated specimens at LdL and Tinguiririca suggest that few living mammals were buried in these deposits.

localities, characterized by many large taxa (table 4.1), derive from sediments deposited in lower-energy environments (compared to Tinguiririca and LdL). Colhuehuapian fossils near Lago Colhué-Huapi occur primarily in infraformational conglomerates and sandstones (Bellosi, 2010; Bellosi and Gonzaléz, 2010). Although these coarse facies are not indicative of consistently low-energy environments, it is noteworthy that these Colhuehuapian deposits represent bedload fluvial systems, whereas fossiliferious strata at LdL appear to have been deposited by flows sufficiently energetic to carry abundant suspended sediments and debris before settling *en masse* (Vallance, 2000; Herriot, 2006). Therefore, it is reasonable to assume that the volcaniclastic deposits at LdL represented denser and higher-energy flows than the bedload fluvial systems at Lago Colhué-Huapi.

The Santa Cruz Formation certainly represents a lower-energy depositional system than the volcaniclastic sediments at LdL. These richly fossiliferous strata are primarily composed of mudstones, fine-grained sandstones, ash-fall tuffs, and reworked tuffs, although the section generally coarsens upward, with sandstones and fine-grained gravels becoming more common (Marshall *et al.*, 1983; Tauber, 1997a; Matheos and Raigemborn, 2012). The Santa Cruz Formation is thought to have been deposited in a low-energy fluvial system with both sheet-like and meandering channels in an emergent lowland (Marshall *et al.*, 1993; Tauber, 1997a; Matheos and Raigemborn, 2012).

*Paleogeographical considerations*

Wertheim (2007) suggested that the high level of endemism in the rodent faunas at LdL (especially compared to coeval faunas in the Argentine foreland) might be related to Andean uplift, with new topographic barriers leading to geographic isolation and habitat fragmentation. Detailed taxonomic analyses of notoungulates have provided further evidence

of taxonomic novelty at LdL faunal (Shockey *et al*., 2012; Luna, Chs. 2-3). The topographic barriers proposed by Wertheim (2007) may help explain the taxonomic novelty at LdL, but this geographic isolation likely cannot account for the scarcity of large-bodied taxa. Intermontane basins, in which fossiliferous deposits at LdL are thought to have accumulated (Herriot, 2006), are known to support diverse mammalian megafauna. For example, the Karewa Group of Kashmir preserves fossil elephants, rhinoceros, horses, giraffes, and bovids (Kotlia, 1985; Nanda, 2008), despite evidence that the surrounding Himalayan peaks impeded migration into the region (Nanda, 2008). The Karewa Group primarily comprises lacustrine and aeolian terraces, representing low-energy depositional environments with little transport sorting potential. The fossil assemblage from Chucal (Santacrucian SALMA; early Miocene) may also represent an intermontane fauna. The fossiliferous Chucal Formation was deposited in a region lower in elevation that its current location on the Altiplano, likely bounded by uplifting borderlands to the east and west (Charrier *et al*., 2005). Several new species from Chucal have been described to date (Croft *et al*., 2004, 2007), but, compared to the fauna from LdL, the assemblage at Chucal has a significantly more uniform size distribution (table 4.1; figs. 4.8, 4.9). At Chucal, taxonomic novelty and potential topographic barriers are not associated with a scarcity of large-bodied taxa.

*Paleoecological considerations*

Paleoecology clearly has the potential to strongly influence faunal composition. Although detailed paleocological studies of the LdL fauna are currently lacking, several inferences merit discussion. Hypsodont and hypselodont rodents at LdL become increasingly predominant up section (Wertheim, 2007), consistent with the spread of abrasive, arid-adapted flora during mid Miocene global cooling (Jacobs *et al*., 1999; Zachos *et al*., 2001).

Rodents with high-crowned (hypsodont) and ever-growing (hypselodont) dentitions commonly (but not exclusively) inhabit open grasslands in arid to semi-arid environments (Verzi *et al.*, 1994; Candela *et al*., 2012), and hypsodonty in the fossil record, among both rodents and ungulates, has been considered an adaptation to grazing associated with the spread of arid grassland environments (Pascual and Odremán-Rivas, 1971; Pascual and Ortiz-Jaureguizar, 1990; Pascual *et al.*, 1996; Flynn *et al.*, 2003). Additional paleobiological evidence suggests that the Tinguiririca fauna inhabited a relatively dry, open environment: body size distributions, ecological parameters, and hypsodonty indexes of fossil taxa have been employed to infer paleoenvironment, and collectively these analyses may document the first open grassland/woodland environment in South America (Croft, 2000, 2001; Flynn *et al.*, 2003; for alternate interpretations see Stromberg *et al*., 2013; Madden, 2014).

The typotherian notoungulates at LdL are all hypselodont (Chs. 2-3). Unlike the rodents at LdL (Wertheim, 2007), typotherians do not become increasingly higher crowned up section; the interatheriids recovered from even the lowest exposures at LdL are already maximally high crowned (hypselodont) (Ch. 2). Although recent studies of enamel microwear/mesowear (Croft and Weinstein, 2008; Townsend and Croft, 2008a) and functional morphology (McCoy and Norris, 2012) suggest that not all hypselodont notoungulates were exclusively open-environment grazers, a broad range of paleoecological analyses incorporating body mass, locomotion, and feeding behavior suggest that typotherians were indeed best suited to open habitats, such as savannahs, grasslands, or semi-desert steppes (see Cassini *et al*., 2012 for summary; for further consideration of enamel microwear, see Billet *et al*., 2009; Townsend and Croft, 2008b). Accordingly, the record of hypsodont and hypselodont rodents and typotherian notoungulates at LdL are generally suggestive of open habitats, and the pattern of "increasing hypsodonty" among

rodents indicates that such environments became more established over time (these preliminary insights are further discussed in Ch. 5).

By comparison, the paleoecology of "type" localities of coeval Colhuehuapian and Santacrucian SALMAs are much better studied. At the Gran Barranca, multiple lines of evidence, including faunal assemblages (Madden *et al*., 2010), sedimentation (Bellosi, 2010), and paleosol composition (Bellosi *et al*., 2010) suggest a relatively warm, moist climate with nearby lowland forests during the Colhuehuapian (early Miocene). Coastal Santacrucian (late early Miocene) paleoenvironments are interpreted as somewhat drier, with the coexistence of both closed and open habitats, consistent with analyses of local flora (Brea *et al*., 2012), sedimentology (Tauber, 1997a; Matheos and Raigemborn, 2012), and faunal composition (Tauber, 1997b; Vizcaíno *et al.*, 2010; Abello *et al*., 2012; Candela *et al*., 2012; Cassini *et al*., 2012; Degrange *et al*., 2012; Kay *et al*. 2012). The preliminary paleoecological inferences of the LdL faunas cannot be readily compared to these thoroughly investigated "type" Colhuehuapian and Santacrucian sequences, but it is certainly possible that dissimilar paleoenvironments affected differences in faunal composition (including size distributions) between LdL and these early Miocene "type" localities. Still, it is unlikely that differences in paleoenvironment alone explain the scarcity of fossils of large-bodied taxa at LdL. After all, dry, open paleoenvironments appear to represent the preferred habitats of most early Miocene notoungulates, including many large toxodontians that are conspicuously scarce or absent at LdL, but abundant in coeval faunas (Cassini *et al*., 2012b).

## SUMMARY

Differential transport in a high-energy depositional environment may have contributed to the predominance of dental and cranial elements of small-bodied taxa recovered from the LdL region. According to this scenario, skeletal remains decaying in an intramontane basin were periodically disturbed, transported, and buried by volcaniclastic mudflows. In these high-energy flows, skeletal components with high mineral densities, such as teeth, mandibles, and skulls, would have a better withstood fragmentation and destruction. Also, small, dense, disarticulated elements would have been more likely to settle quickly in debris and hyperconcentrated flow deposits close to where transport began, while larger, articulated elements would have been preferentially transported downstream. This interpretation is supported not only by previous taphonomic studies, but also by the contrasts between the LdL fossils and coeval faunas. At Chucal and "type" Colhuehuapian and Santacrucian localities, which are characterized by lower-energy depositional settings, fossil assemblages include a greater proportion of large taxa (and, in the case of Chucal, a less pronounced bias towards cranial elements). Conversely, fossils from LdL and Tinguiririca, preserved in high-energy lahars (Wyss *et al*., 1994; Charrier *et al*., 1996; Herriot, 2006), are characterized by a striking overrepresentation of cranial elements of small-bodied taxa.

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Chapter 5. Summary and Synthesis of Laguna del Laja Faunas

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# Chapter 5. Summary and Synthesis of Laguna del Laja Faunas

This chapter has three objectives. It begins with a brief summary of the typotherians from Laguna del Laja (LdL), emphasizing their stratigraphic occurrences. This is followed by a report of two dentitions from LdL that are referred to *Astrapothericulus iheringi* (Ameghino, 1899). The chapter concludes with an overview of rodent and ungulate faunas from LdL, including discussions of their biogeographic and biostratigraphic correlations, the strong pattern of endemism observed at the genus and species levels, and the record of hypsodonty/hypselodonty and its paleoecological and evolutionary ramifications.

## Newly described typotherian notoungulates

Typotherians have been recovered from units $Tcm_1$, $Tcm_3$, and $Tcm_4$ (following the stratigraphy of Herriott, 2006) of the Cura-Mallín Formation (CMF) southeast of LdL, a stratigraphic sequence spanning ~20-15 Ma (fig. 5.1). These well-sampled units of the CMF have produced two new interatheres (INT A and INT B) and two new hegetotheres (HEG A and PACH B) (figs. 5.1; Chs. 2-3). A third new interathere (INT C) is described on the basis of two dentitions, one from the CMF immediately north of LdL, and one from the Abanico Formation near Río Las Leñas (~240 km NNE of LdL) (see fig. 1.2). Though the age of the former dentition is poorly constrained, the latter is dated to ~20 Ma, correlating temporally with the lowest exposures of CMF southeast of LdL (Ch. 2). Four dentitions from LdL are referred to *Protypotherium praerutilum* (Interatheriinae, Interatheriidae) (Ch.2), and the occurrence of *Pachyrukhos moyani* (Pachyrhukhinae, Hegetotheriidae) is also tentatively recognized (Ch.3). Within the CMF, interatheriids are restricted to the lower units ($Tcm_1$ and basal horizons of $Tcm_3$), whereas hegetotheriids range further up section (including $Tcm_4$) (fig. 5.1). This likely represents a sampling artifact rather than a true paleoecological trend, particularly as the upper units of the CMF have yielded fewer fossils than the lower units (see fig. 1.6), and a probable interatheriid dentition occurs in the overlying Trapa Trapa Formation (TTF) (fig. 5.1).

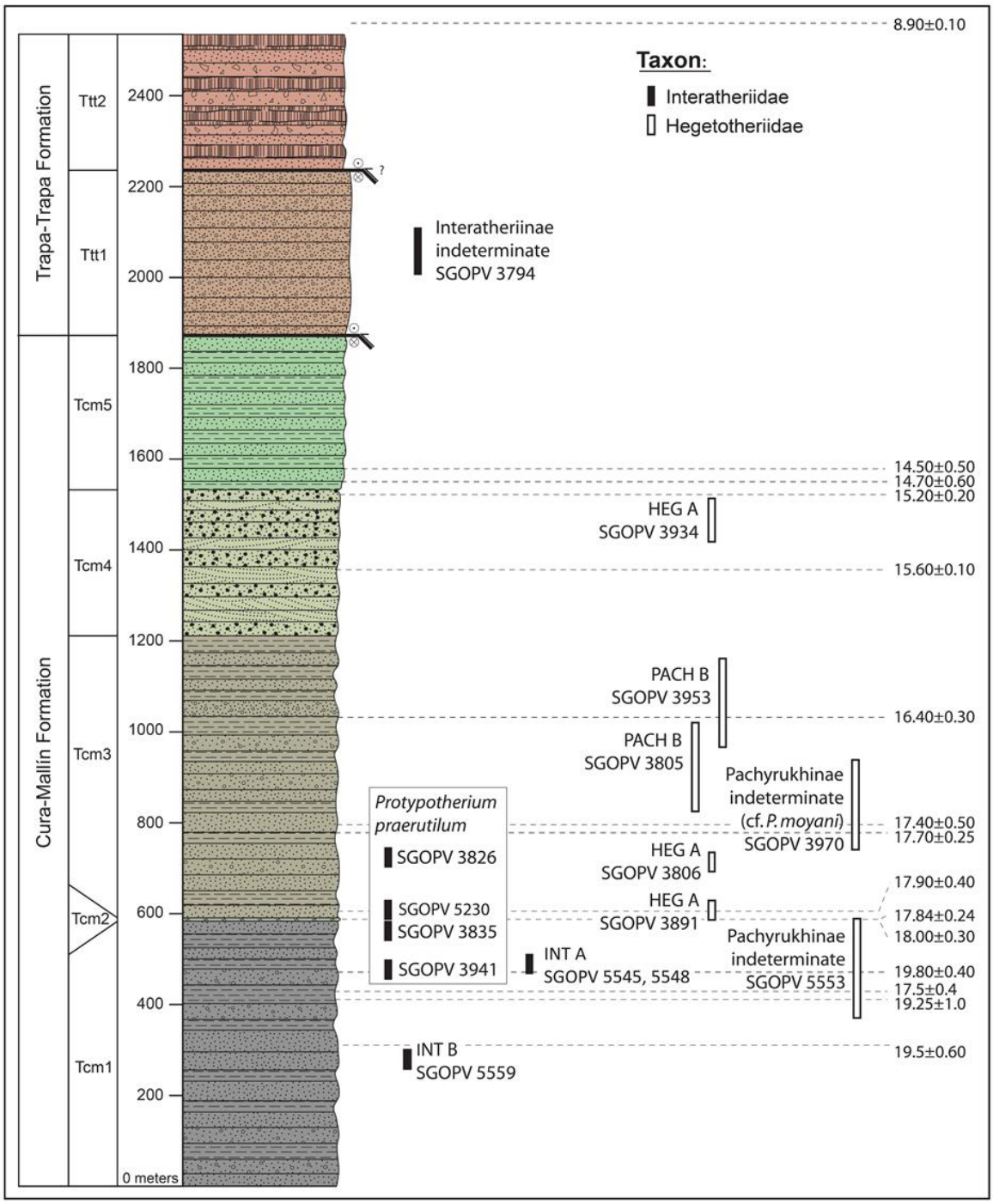


FIGURE 5.1. Stratigraphic position of typotherian notoungulate fossils from the Cura Mallín and Trapa Trapa formations in the region southeast of Laguna del Laja. Each bar corresponds to the stratigraphic position of a particular locality, most of which are associated with a single specimen (indicated by SGOPV #). The vertical height of each bar represent the level of uncertainty in stratigraphic position (short bars = well-constrained; longer bars = moderately to poorly constrained). The stratigraphic positions of $^{40}Ar/^{39}Ar$ ages are also indicated. See fig. 1.6 for stratigraphic column legend.

## Record of *Astrapothericulus iheringi* from Laguna del Laja

Two dentitions from LdL are referred to Astrapotheria, an extinct group native South American ungulates known from the Paleocene (Soria and Powell, 1981) to the middle Miocene (Johnson and Madden, 1997, Goillot *et al*., 2011; Vallejo-Pareja *et al*., 2015). The peculiarities of astrapotheres are epitomized in the words of William B. Scott (1937, pg. 309): "The skeleton is one of paradoxes and contradictions…especially because no animal now living is in the least like these extraordinary creatures." These "paradoxes" include retracted nasals (especially pronounced in later-diverging taxa, indicating the presence of a trunk-like proboscis), immense canines, rhino-like cheek teeth, and, for some taxa, extremely large bodies with disproportionately slender limbs (Scott, 1937; Cifelli, 1993). Astrapotheres were among the largest mammals in South America from the middle Eocene until the middle Miocene (Johnson and Madden, 1997; Kramarz and Bond, 2008, 2011, 2013; Cassini *et al*., 2012a, 2012b; Vallejo-Pareja *et al*., 2015); recent body mass estimates of the prodigious *Astrapotherium giganteum* (early Miocene) exceed 3,000 kg (Kramarz and Bond, 2011)[5]. The affinities between astrapotheres and other groups of South American ungulates are uncertain (see Soria, 1988; Cifelli, 1993; Horovitz, 2004; Billet, 2010; Billet *et al*., 2015), but recent phylogenetic analyses have helped clarify the relationships among the 16 currently recognized astrapothere genera (e.g., Cifelli, 1993; Johnson and Madden, 1997;

[5] Indeed, considering the bulk of *Astrapotherium*, a name meaning "lightning beast," Scott (1937, pg. 309) remarked on yet another paradox: "A more inappropriate and infelicitous name could hardly have been selected, for anything less lightning-like than this strange beast cannot be imagined."

Kramarz and Bond; 2009, 2011; Bond *et al*., 2011; Vallejo-Pareja *et al*., 2015). These studies provide robust support for two Miocene sub-clades: Uruguaytheriinae (including *Granastrapotherium*, *Xenastrapotherium*, *Hilarcotherium*, and *Uruguayatherium*) and Astrapotheriinae (including *Astrapotherium* and *Astrapothericulus*; *sensu* Kramarz and Bond, 2009).

## SYSTEMATIC PALEONTOLOGY

ASTRAPOTHERIA Lydekker, 1894

ASTRAPOTHERIIDAE Ameghino, 1887

ASTRAPOTHERIINAE Simpson, 1945

*Astrapothericulus* Ameghino, 1902

*Astrapothericulus iheringi* (Ameghino, 1899)

SYNONYMY: *Astrapotherium iheringi* Ameghino, 1899, pg. 5

*Astrapotherium hebetatum* Ameghino, 1899, pg. 5

LECTOTYPE: MACN-A 52-419, fragment of left maxilla bearing P3-M3.

TYPES IN SYNONMY: MACN-A 52-405, syntype of *Astrapotherium hebetatum*, a partial mandible with p4-m1, and several isolated teeth from more than one individual.

NEWLY REFERRED MATERIAL: SGOPV 3961, fragmentary mandible bearing left p4-m3 (m3 partial) and fragmentary right p4-m2, and associated incisor (i2 or i3?) and lower right canine (fig. 5.2). SGOPV 3860, isolated lower left canine.

DISTRIBUTION: Early Miocene, Chilean and Argentine Patagonia. Cerro Bandera Formation (Colhuehuapian SALMA, early Miocene) in Neuquenén Province, Argentina.

Pinturas Formation (basal Santacrucian SALMA, late early Miocene), Santa Cruz Province, Argentina (Kramarz, 2009). Basal Santa Cruz Formation (possibly post-Colhuehuapian, pre-Santacrucian SALMA; late early Miocene) in Última Esperanza Province, Chile (Bostelmann *et al*., 2013). Specimens from the LdL region, SGOPV 3860 (from locality C-04-6) and SGOPV 3961 (from locality C-04-26), were both recovered from unit $Tcm_3$ of the CMF at Estero Trapa Trapa West, with bracketing radioisotopic dates suggesting an age of ~17-16 Ma (see fig. 5.3).

DISCUSSION: SGOPV 3860 and SGOPV 3961 are clearly referable to the Miocene clade Astrapotheriinae (*sensu* Kramarz and Bond, 2009), based on the presence of a strong labial flexid on m1-3 and basal cingulae on the lower molars (lingually and labially) (Kramarz and Bond, 2009). Astrapotheriinae includes only *Astrapotherium* and *Astrapothericulus*, both recently revised (Kramarz, 2009; Kramarz and Bond, 2010). Both specimens from LdL possess diagnostic characters of *Astrapothericulus iheringi*, including: 1) small size relative to other astrapotheriines (comparable to *A. iheringi* and *Astrapotherium? ruderarium*); and 2) slender lower canines with concave lingual faces (whereas in *A. ruderarium* the lower canines are more robust with convex lingual faces). SGOPV 3961, the more complete dentition, displays additional diagnostic morphology, including: 3) a conspicuous labial flexid on p4 (though not as pronounced as in *A. ruderarium*); 4) slender incisors; and 5) prominent basal cingula on the lower cheek teeth.

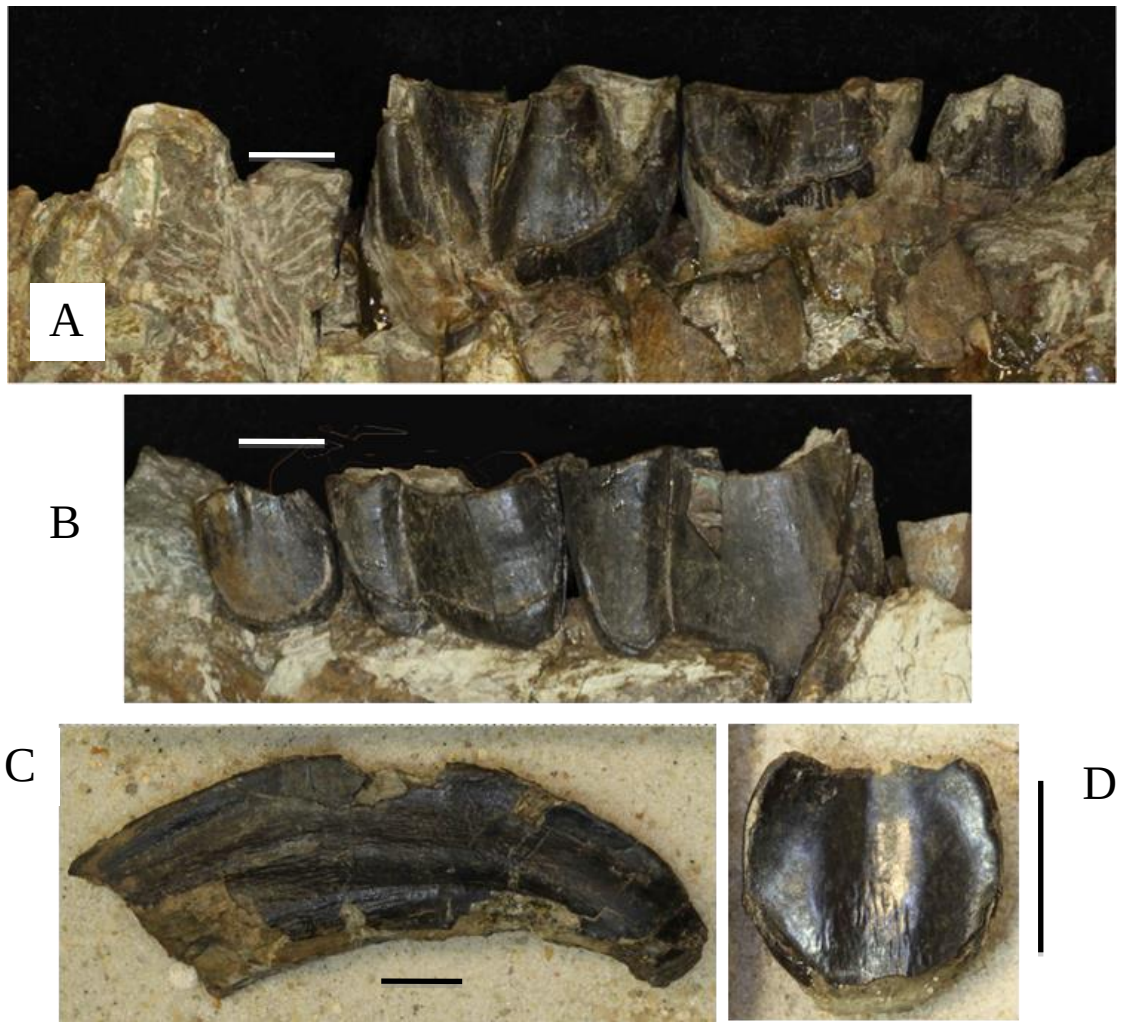


FIGURE 5.2. SGOPV 3961, *Astrapothericulus iheringi*. **A**: Left p4-m3 (m3 broken) in lingual view. **B**: Left p4-m2 in labial view. **C**: Lower right canine in lingual view. **D**: Incisor (i2 or i3?) in lingual view. Scale bars = 1 cm.

**Biogeographic and biostratigraphic considerations**

Six typotherians, one toxodontian, one astrapothere, and 21 rodents have been identified to the species level at LdL (tables 5.1, 5.2). Here I consider the newly described ungulates from LdL, and provide summary comments about the rodent faunas (described by Wertheim, 2007).

A majority of rodents and ungulates at LdL represent novel genera (fig. 5.3). The biogeographic and biostratigraphic implications of these new taxa are generally limited, since they often pertain to clades with wide distributions. For example, in the phylogeny proposed herein (Ch.2; see fig. 5.7), Interatheriidae gen. *et* sp. *nov*. A (INT A) is nested within a clade that also includes *Protypotherium, Progaleopithecus,* and *Miocochilius* (informally recognized as "*Protypotherium* and allies"). These taxa range in age from late Oligocene to late Miocene, and are distributed as far north as Colombia (*Miocochilius*; Stirton, 1953) and as far south as Patagonia (*Protypotherium*; Ameghino, 1887; Sinclair, 1909). Thus the occurrence of Int A at LdL does little to help circumscribe the geographic or temporal range of "*Protypotherium* and allies." Consequently, the following discussion highlights taxa from LdL referred to previously recognized genera, the distribution of which consistently suggest at least some degree of Patagonian faunal association, and permit direct biostratigraphic comparisons to South American Land Mammal "Ages" (SALMAs).

Before discussing these Patagonian affinities, however, one newly described typotherian genus merits discussion for different reasons. Interatheriinae gen. *et* sp. *nov*. C (INT C) is described (Ch. 2) on the basis of two dentitions, one (SGOPV 3974) from the CMF several km north of LdL, and the other (SGOPV 3210) from the Abanico Formation

near Río Las Leñas (~240 km NNE of LdL) (fig. 5.4). Together, these volcaniclastic sequences are exposed from ~33°-39° S in the Andes of central Chile. The Abanico Formation (~33°-36° S) and CMF (~36°-39° S) are roughly correlative (Charrier *et al*., 2002), but these formations were deposited over different (though partly overlapping) time spans (Abanico Fm.: Late Cretaceous to middle Miocene [Mosolf, 2013]; CMF: latest Oligocene to late Miocene [Jordan *et al*., 2001; Herriott, 2006; Flynn *et al*., 2008]). Several mammal faunas have been recovered from the Abanico Formation, likely ranging in age from late Eocene to early Miocene (summarized in Flynn *et al*., 2012); most fossils described to date are early Oligocene in age (Wyss *et al*., 1993, 1994; Hitz *et al*., 2000, 2006; Flynn *et al*., 2003; Croft *et al*., 2003; Reguero *et al*., 2003a; Bertrand *et al*., 2012), but Miocene specimens notably include a platyrrhine skull from Las Leñas (*Chilecebus carrascoensis*) (Flynn *et al*., 1995). INT C is therefore among the few Miocene-aged taxa described from the Abanico Formation, and it also the first species that occurs in *both* the CMF and the Abanico Formation. This co-occurrence is particularly fortuitous because it permits biochronolgic correlation. The age of SGOPV 3974 (from LdL) is uncertain (see Ch. 2), whereas an $^{40}Ar/^{39}Ar$ date of 20.09 ± 0.27 Ma derives from the same house-sized block as SGOPV 3210 (from Las Leñas, Abanico Fm.). The dentition from LdL is likely of similar age (i.e., ~20 Ma), as this is consistent with the age of the lowest exposures of the CMF southeast of LdL, from which two other newly described interatheriids have been recovered (figs. 5.1, 5.3). In addition to facilitating temporal correlation, the co-occurrence of INT C at LdL and Las Leñas provides the first potential indication of a more widespread early Miocene "Andean fauna" in central Chile. Further study of coeval fossils from the CMF and Abanico Formation will help to establish the extent of such taxonomic similarities, and their possible paleoecological, biostratigraphic, and biogeographic implications.

TABLE 5.1. Taxonomic list of rodents and ungulates that have been described from Laguna del Laja

- Notoungulata
  - Toxodontia
    - Leontiniidae
      - *Colpodon antucoensis*
  - Typotheria
    - Interatheriidae
      - Interatheriinae
        - *Protypotherium praerutilum*
        - Interatheriinae gen. *et* sp. *nov*. A
        - Interatheriinae gen. *et* sp. *nov*. B
        - Interatheriinae gen. *et* sp. *nov*. C
        - Interatheriinae indet.
    - Hegetotheriidae
      - "Hegetotheriinae"
        - Hegetotheriidae gen. *et* sp. *nov*. A
      - Pachyrukhinae
        - Pachyrukhinae gen. *et* sp. *nov*. B
        - Pachyrukhinae indet. (cf. *Pachyrukhos moyani*)
        - Pachyrukhinae indet.
- Astrapotheria
  - Astrapotheriidae
    - Astrapotheriinae
      - *Astrapothericulus iheringi*
- Rodentia
  - Octodontoidea
    - Echimyidae
      - *Acarechimys* n. sp
      - Echimyidae gen. *et* sp. *nov*. I
      - Echimyidae gen *et* sp. *nov*. II
      - Echimyidae gen *et* sp. *nov*. III
      - Echimyidae gen *et* sp. *nov*. IV
      - Echimyidae gen. *et* sp. *nov*. V
      - Echimyidae gen. *et* sp. *nov*. VI
      - *Prostichomys* n. sp. I
      - *Prostichomys* n. sp. II
      - *Protacaremys* n. sp. I
      - ?*Protacaremys* sp.
      - *Maruchito* n. sp
  - Caviodea
    - Dasyproctidae
      - *Neoreomys* n. sp.
      - Dasyproctidae gen. *et* sp. *nov*. I
      - Dasyproctidae gen. *et* sp. *nov*. II
      - Dasyproctidae gen. *et* sp. *nov*. III
      - Dasyproctidae gen *et* sp. *nov*. IV
      - ?*Scleromys* n. sp.
    - Eocardiidae
      - *Luantus* n. sp
      - Eocardidae indet.
  - Chinchilloidea
    - Chinchillidae
      - *Prolagostomus* n. sp. I
      - *Prolagostomus* n. sp. II
      - *Prolagostomus* sp.

TABLE 5.2. Rodents and ungulate taxa occurring in each unit of the Cura Mallín and Trapa Trapa formations at Laguna del Laja. See figs. 5.1 and 5.3 for stratigraphic relationships of each unit. See fig. 1.6 for descriptions of each unit. $Tcm_3$ is divided into two sections, the "lower beds" exposed at Estero Trapa Trapa East (TTE) and the "upper beds" exposed at Estero Trapa Trapa West (TTW).

| Rodentia | Notoungulata and Astrapotheria |
|---|---|
| $Ttt_1$ | |
| Dasyproctidae gen *et* sp. *nov*. IV | Interatheriinae indet. |
| $Tcm_5$ | |
| Dasyproctidae gen et sp. nov. III | |
| *Prolagostomus* sp. | |
| $Tcm_4$ | |
| *Prolagostomus* n. sp. II | Hegetotheriidae gen. *et* sp. *nov*. A |
| Echimyidae gen *et* sp. *nov*. II | |
| $Tcm_3$ (upper beds; TTW) | |
| *Luantus* n. sp | Pachyrukhinae gen. *et* sp. *nov.* B |
| *Prolagostomus* n. sp. I | Pachyrukhinae cf. *P. moyani* |
| Echimyidae gen. *et* sp. *nov*. I | *Astrapothericulus iheringi* |
| Echimyidae gen. et sp. nov. III | |
| Echimyidae gen. *et* sp. *nov*. IV | |
| Echimyidae gen. *et* sp. *nov*. V | |
| ?*Scleromys* n. sp. | |
| Eocardidae indet. | |
| $Tcm_3$ (lower beds; TTE) | |
| *Luantus* n. sp | Hegetotheriidae gen. *et* sp. *nov*. A |
| *Prostichomys* n. sp. I | *Protypotherium praerutilum* |
| *Prostichomys* n. sp. II | |
| Dasyproctidae gen. *et* sp. *nov*. I | |
| Dasyproctidae gen. *et* sp. *nov*. II | |
| *Acarechimys* n. sp | |
| *Maruchito* n. sp | |
| $Tcm_1$ | |
| Echimyidae gen. *et* sp. *nov*. VI | Interatheriidae gen. *et* sp. *nov*. A |
| *Neoreomys* n. sp. | Interatheriidae gen. *et* sp. *nov*. B |
| ?Protacaremys sp. | Interatheriidae gen. *et* sp. *nov*. C* |
| | *Protypotherium praerutilum* |
| | Pachyrukhinae indet. |
| | *Colpondon actucoensis* |

*The stratigraphic position of this taxon at Laguna del Laja is unknown, but its age at Las Leñas suggests temporal correlation with the lowest unit exposed at Laguna del Laja.

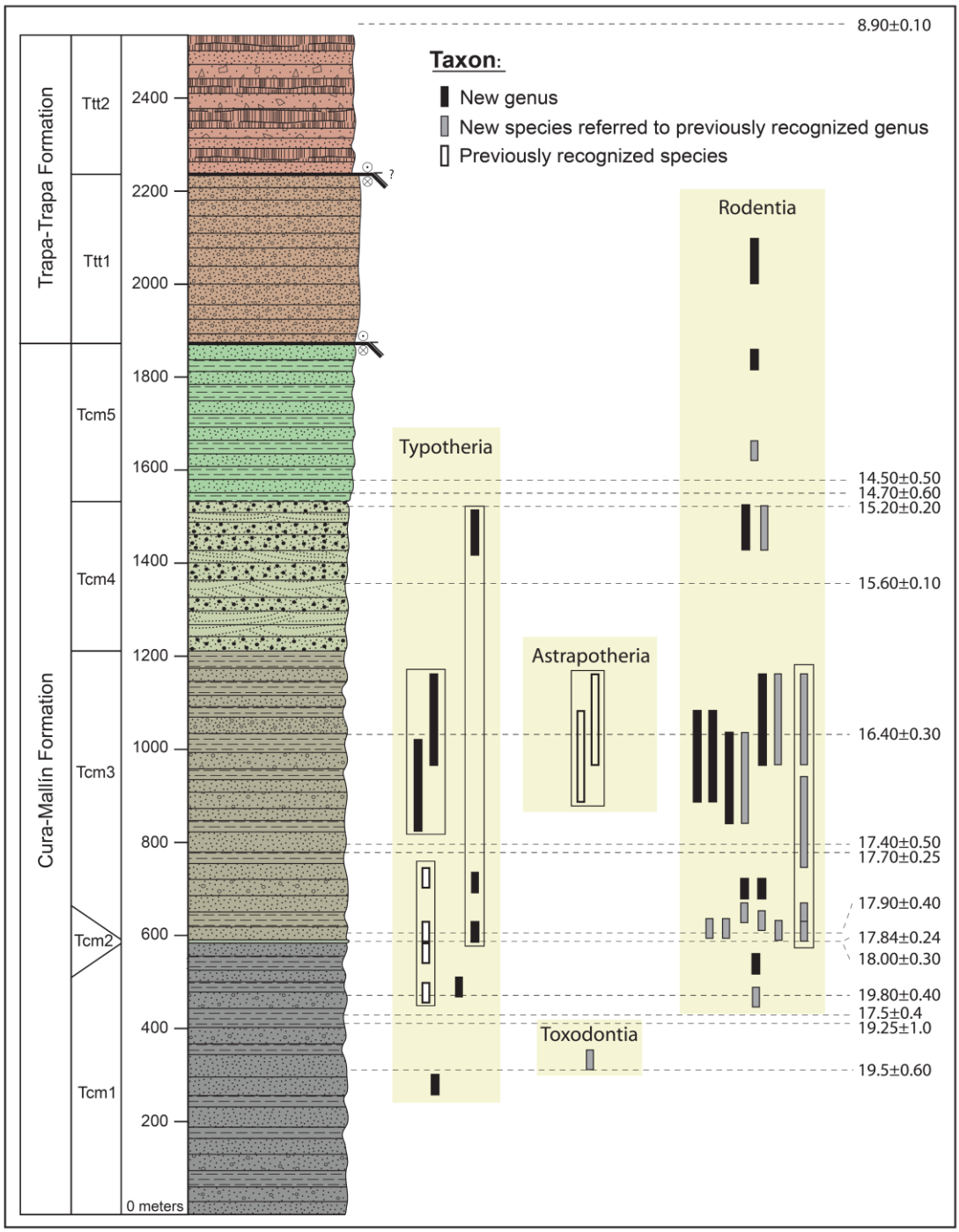


FIGURE 5.3. Stratigraphic position of rodent and ungulate fossils from the Cura Mallín and Trapa Trapa formations in the region southeast of Laguna del Laja. Only specimens confidently identified to species-level are included. Each bar corresponds to the stratigraphic position of a particular locality. If a locality records more than one taxon, a different bar is shown for each taxon. Bars that are "boxed in" indicate multiple occurrence of the same taxon at different localities.The vertical height of each bar represent the level of uncertainty in stratigraphic position (short bars = well-constrained; longer bars = moderately to poorly constrained). The stratigraphic positions of $^{40}Ar/^{39}Ar$ ages are also indicated. See fig. 1.7 for stratigraphic column legend.

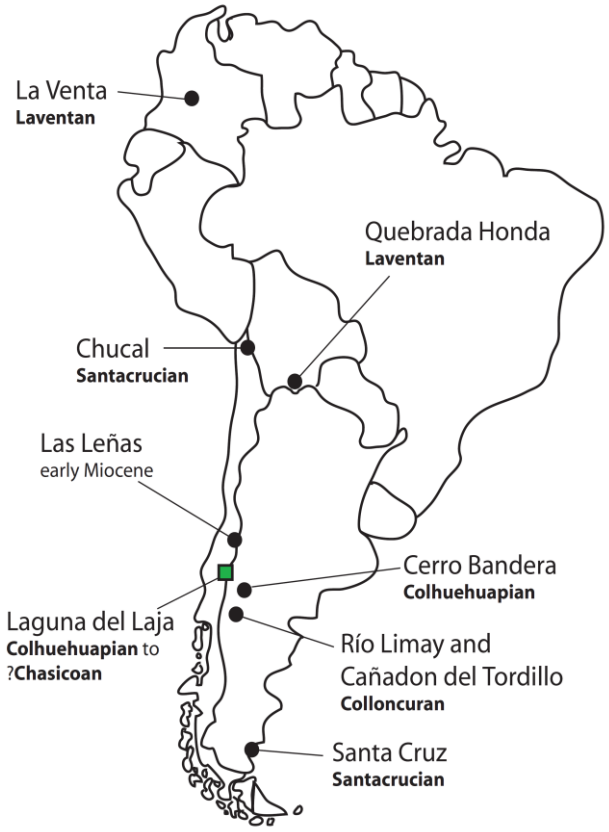


FIGURE 5.4. Map of South America indicating fossil localities discussed in the text. The SALMAs associated with these faunas are highlighted in bold type. The fauna from Las Leñas has yet to be correlated to a SALMA, but preliminary assessments, combined with a single $^{40}Ar/^{39}Ar$ date of 20.09 ± 0.27 Ma (Flynn *et al*., 1995), suggest an early Miocene age. Most fossils treated in the present study were recovered from the Laguna del Laja region (green square); one specimen from Las Leñas is also described.

The taxa from LdL referred to previously recognized genera suggest at least some degree of association with Patagonian faunas. *Astrapotheriuculus iherngi*, for example, has previously been reported only from the early Miocene of Patagonia (Kramarz, 2009; Bostelmann *et al*., 2013). The earliest, Colhuehuapian-aged specimens of this taxon are from the Cerro Bandera region of northern Patagonia (Neuquén Province, Argentina) (Kramarz, 2009) (fig. 5.4), while slightly younger (post-Colhuehuapian to basal Santacrucian) occurrences are reported from southern Patagonia in Argentina (Kramarz, 2009) and Chile (Bostelmann *et al*., 2013). The two astrapothere dentitions reported above, likely ranging in age from 16-17 Ma, represent the first occurrence of *A. iherngi* outside of Patagonia (LdL is ~215 km northwest of the Cerro Bandera; fig. 5.4), and may extend the youngest record of this taxon from the basal Santacrucian (Kramarz, 2009) to the upper Santacrucian (fig. 5.5).

A similar pattern has previously been documented for *Colpodon*, which until recently was known only from the early Miocene (Colhuehuapian SALMA) of Argentine Patagonia (Shockey *et al*., 2012). Newly described from Laguna del Laja, *C. antucoensis* (~20-19.5 Ma) represents the northernmost occurrence of this genus (Shockey *et al*., 2012), and possibly the youngest (*Colpodon* is known from the Colhuehuapian SALMA, which has recently been calibrated to ~21.1–20.1 Ma at its "type" locality [Dunn *et al*., 2013]) (fig. 5.5).

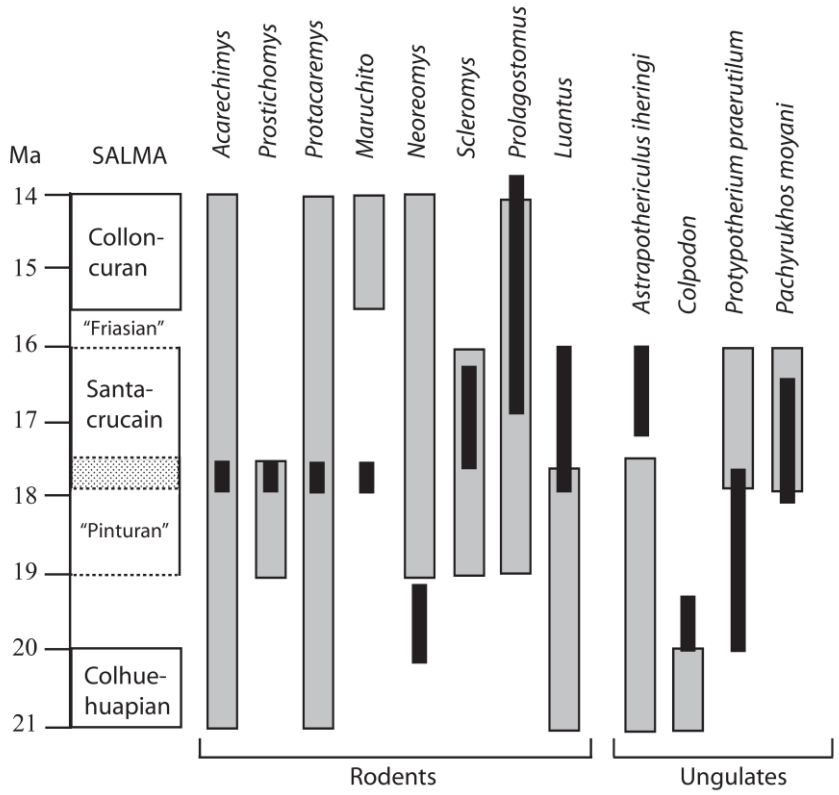


FIGURE 5.5. Temporal distributions of genera that occur at both Laguna del Laja (black bars) and Patagonian localities (grey bars). "Age" ranges of taxa from Patagonian localities indicate their occurrence in faunas associated with each SALMA, not necessarily their true temporal distribution. Age ranges of taxa from Laguna del Laja (black bars) are approximate, encompassing uncertainties in stratigraphic position and geochronologic data (see figs. 5.1, 5.3). Sources for SALMA temporal calibrations: Colloncuran (Flynn and Swisher, 1995), Santacrucian (Perkins *et al*., 2012; Fleagle *et al*., 2012 [note: ages for coastal localities of Santa Cruz Formation]), "Pinturan" and Colhuehuapian (Dunn *et al*., 2013). Stippled lines indicate uncertainty in boundary ages; stippled rectangle between Santacrucian and "Pinturan" indicates potential overlap of these SALMAs (following Fleagle *et al*., 2012; Dunn *et al*., 2013). Temporal distribution of Patagonian rodents from Wertheim, 2007, with ranges of *Acarechimys*, *Neoreomys*, *Protacaremys*, and *Prolagostomus* modified according to Kramarz *et al*., 2010, 2011 and Vucetich *et al*., 2010. Temporal distributions of Patagonian ungulates discussed in text (with references).

*Protypotherium praerutilum* is one of the best-represented species at LdL, with four dentitions referred to this taxon ranging in age from ~20-17.7 Ma. *P. praerutilum* is primarily known from the late early Miocene of southern Patagonia (Santacrucian SALMA) (e.g., Ameghino, 1887, 1889, Sinclair, 1909; Tauber 1996, 1997), but it has also been reported from the middle Miocene (Colloncuran SALMA) of northern Patagonia (Río Limay region of Argentina; ~300 km SSE of LdL) (Rolleri *et al*., 1948)[6]. Accordingly, *P. praerutilum* in the LdL region represents the northernmost and oldest confirmed record of this taxon (fig. 5.4). The true geographic and temporal range of *P. praerutilum*, however, is difficult to ascertain (see Ch. 2); there are poorly substantiated reports of *Protypotherium* sp. from well north of LdL in Argentina (e.g., Cabrera and Kraglievich, 1931; Bond and Lopez, 1996; Linares, 2004; Tauber, 2005) and from earlier than the Santacrucian SALMA (Kramarz *et al*., 2005). The taxonomic assessment of *Protypotherium* provided herein (Ch. 2) is based primarily on collections from Argentine Patagonia; a more thorough revision is required to better understand the temporal and geographic distribution of *Protypotherium* and its constituent species. Despite these limitations, the overall record suggests that *Protypotherium* may have been restricted to Patagonia in the early and middle Miocene, and that its range shifted northward in the late Miocene (Bond and Lopez, 1996; Kramarz *et al*., 2005; Tauber 2005) (possibly as far as Venezuela; Linares, 2004). The early Miocene occurrence of *P. praerutilum* at LdL, therefore, corresponds to a time during which *Protypotherium* was most common in Patagonia.

[6] I have not examined Colloncuran fossils attributed to *P. praerutilum*, but Tauber (2005) suggests that they are instead referable to juvenile specimens of *P. australe*.

A brief comment concerning SGOPV 3970 (Pachyrukhinae indeterminate) is warranted. Although this partial skull could not be confidently identified to the level of species, it compares very favorably with *Pachyrukhos moyani*, and may indeed pertain to this taxon (Ch. 3). Like *Protypotherium*, *Pachyrukhos* needs to be revised (see Ch. 3), making the distribution of this genus uncertain, but certainly it is best known from the late early Miocene of Argentine Patagonia (Santacrucian SALMA) (Ameghino, 1885, 1887; Sinclair, 1909). Here, yet again, the possible occurrence of *P. moyani* at LdL may represent the northern range limit for a typically Patagonian taxon, and also provides a "typical" Santacrucian taxonomic signal in temporally equivalent horizons at LdL (fig. 5.5).

Well-studied, early and middle Miocene faunas are also known from the Andes of Chile (Chucal; early Miocene Santacrucian SALMA) (Flynn *et al*., 2002a; Croft *et al*., 2004, 2007), Bolivia (Quebrada Honda; middle Miocene Laventan SALMA) (see Croft, 2007 for recent faunal summary), and Colombia (La Venta; middle Miocene Laventan SALMA) (see Kay *et al*., 1997 for recent summary) (fig. 5.4). Faunas from LdL include three (perhaps four, including *Pachyrukhos*) ungulate genera in common with coeval Patagonian faunas, but, conversely, none in common with faunas from Chucal, Quebrada Honda, or La Venta. This pattern is particularly striking considering that LdL is roughly equidistant from the Santacrucian localities of Chucal (~2000 km north of LdL; no ungulate genera in common) and Santa Cruz (~1500 km SSE of LdL; possibly 2 ungulate genera in common) (fig. 5.4). A similar Patagonian correlation is observed among rodents: of the eight rodent taxa at LdL referrable to previously recognized genera (*Acarechimys*, *Prostichomys*, *Protacaremys*, *Maruchito*, *Neoreomys*, *Scleromys*, *Prolagostomus*, and *Luantus*), all eight are also known from Patagonian localities (Wertheim, 2007) (fig. 5.5), whereas only two are recorded at Chucal (*Neoreomys*, *Acarechimys*; Croft *et al*., 2007), two at Quebrada Honda (*Neoreomys*,

*Prolagostomus*; Croft, 2007), and three at La Venta (*Scleromys*, *Neoreomys*, *Acarechimys*; Madden *et al*., 1997). This pattern may partly reflect the fact that Patagonian fossil localities are more numerous and better studied; perhaps more taxonomic similarities between LdL and middle/low latitude Andean localities will be discerned as more taxa are described. Even so, these similarities at the genus-level are indicative of relatively strong faunal connections with Patagonia. A similar pattern is observed at higher taxonomic levels. For example, four interatheriid taxa are recorded from horizons of early Miocene age at LdL and Las Leñas, including three newly described taxa (INT A, INT B, INT C) and *Protypotherium praerutilum* (fig. 5.1). Interatheriids are also known from the early Miocene of Patagonia (Colhuehuapian SALMA: *Cochilius*,?*Protypotherium*[7]; Ameghino, 1902; Simpson, 1932; Bordas, 1939; Barrio *et al*., 1986; Kramarz *et al*., 2005) and are especially abundant in the late early Miocene of Patagonia (Santacrucian SALMA: *Interatherium*, *Protypotherium*; Ameghino, 1887; Sinclair, 1909; Tauber, 1996; Flynn *et al*., 2002b) (see fig. 5.7), but interatheriids are conspicuously absent at Chucal (late early Miocene Santacrucain SALMA) (Croft *et al*., 2004).

These taxonomic similarities between faunas from LdL and Patagonia permit a degree of direct biostratigraphic correlation to the SALMA sequence (most of which was established on the basis of Patagonian fossil collections), but such efforts are hindered when genera at LdL are older or younger than their Patagonian counterparts (e.g., *Protypotherium praerutilum*, *Maruchito*), or when genera are long-lived in Patagonia (e.g., *Acarechimys*, *Protacaremys*) (fig. 5.5). Still, these combined biostratigraphic and geochronologic data

[7] Colhuehuapian records of *Protypotherium* are of uncertain validity, in light of the taxonomic assessment herein (Ch. 2), but these fossils nonetheless certainly represent interatheriids.

generally support correlations to "Pinturan" [8] and Santacrucian faunas (fig. 5.5): *Prostichomys* is recorded from the "Pinturan" of Patagonia and occurs cotemporally at LdL; Patagonian records of *Scleromys* range from "Pinturan" to Santacrucian, and the age of this taxon at LdL is consistent with a Santacrucian occurrence; the distributions of *Luantus* and *Astrapothericulus* at LdL extend the youngest record of this taxon from "Pinturan"/basal Santacrucian to upper Santacrucian; *Pachyrukhos moyani* is best (and perhaps only) known from the Santacrucian of Patagonia, and its possible occurrence at LdL falls within the same timespan (fig. 5. 4) (age ranges of Patagonian rodents from Wertheim, 2007; distributions of *Astrapothericulus* and *Pachyrukhos moyani* discussed above). The occurrence of *Colpodon* also provides a taxonomic link to the Colhuehuapian, though the record of this genus at LdL is slightly younger than the "type" Colhuehuapian fauna from the Gran Barranca of Argentine Patagonia (Dunn *et al*., 2013), and the distribution of *Prolagostomus* at LdL is temporally consistent with the Santacrucian and Colloncuran record of this taxon in Patagonia (Wertheim, 2007; Kramarz *et al*., 2011) (fig. 5.5).

Although the preponderance of newly described taxa from LdL precludes a more thorough taxonomic comparison between the LdL faunas and those of Patagonia, it has other biogeographic implications.

[8] The "Pinturan" has been thought to represent either a basal Santacrucian fauna or a pre-Santacrucian post-Colhuehuapian fauna (see recent summaries and discussions in Kramarz *et al*., 2010; Fleagle *et al*., 2012; Dunn *et al*., 2012). Here, the "Pinturan" is regarded as generally older than, but overlapping with, the Santacrucian (following Fleagle *et al*., 2012; Dunn *et al*., 2012).

**Endemism at Laguna del Laja**

Of the 26 taxa at LdL confidently identified at the species level, 24 are new (15 of them at the level of genus). This level of endemism is striking, especially considering the geographic proximity of LdL to several coeval faunas (fig. 5.4). In particular, the northern Patagonian localities of Cerro Bandera (Kramarz *et al*., 2005) Cañadon del Tordillo (Vucetich *et al*., 1993), and Río Limay (Rolleri *et al*., 1948), which produce faunas ranging in age from early to middle Miocene (Colhuehuapian and Colloncuran SALMAs), all lie within ~370 km of LdL (fig. 5.4). Although these faunas share some taxonomic similarities (discussed above; see also fig. 5.5), only a single species from LdL is also recorded at these Argentine localities: *Astrapotheriuculus iheningi* at Cerro Bandera (Kramarz, 2009) (but see footnote 2). Such prevalent endemism is all the more remarkable considering that all the fossils from LdL that have been referred to previously known genera suggest at least some level of Patagonian faunal association.

The present geographic location of LdL and evidence that the CMF accumulated in an intra-arc setting (e.g. volcaniclastic deposits associated with lahars, numerous interbedded tuffs and ignimbrites), suggest that the steep topography of the Andes cordillera may have provided a certain degree of geographic isolation that accounts for the endemism observed in the LdL faunas. This proposal invokes the ancient topology and structure of the Andes, rather than the range's current configuration. Although subduction-related orogenesis and magmatism along the western margin of South America dates back to at least the early Jurassic (Harmon and Rapela, 1991; Oncken *et al*., 2006), recent studies suggest a complex uplift history, the timing of which is open to varying interpretations. Structural, tectonic, and geochronologic studies of the cordillera between ~34°-37.5° S (LdL is at ~37.5° S) suggest

that the onset of tectonic shortening and uplift in this region of the cordillera may have commenced anywhere from the late Eocene (Mosolf, 2013), to the early Miocene (Charrier *et al*., 2002; Kay *et al*., 2005), to the middle/late Miocene (Jordan *et al*., 2001; Heriiott, 2006). In the LdL region, the CMF and TTF are commonly thought to have been deposited during a time of extension, but preceded and followed by episodes of folding and uplift (Jordan *et al*., 2001; Herriott, 2006; Melnick *et al*., 2006; Flynn *et al*., 2008)

Rodent faunas from LdL evince a pattern of "increasing endemism" up section in the CMF; fossils from lower units exhibit greater taxonomic and morphological similarities to their coeval Patagonian counterparts than those from higher stratigraphic levels (where a greater proportion of new genera occur) (Wertheim, 2007). Given the wide range of suggested ages for uplift in this region, Wertheim (2007) suggested that "increasing endemism" might indicate when the Andes became an effective isolating barrier. Accordingly, it was argued that uplift commenced ~18 Ma, after which novel genera become more common (Wertheim, 2007) (fig. 5.6). It is important to note, however, that only two rodent taxa (out of 23) from LdL are older than ~18 Ma.

The present study includes seven ungulates identified to the species level from LdL[9]; five of these taxa are older than ~18 Ma, three of which represent novel genera (fig. 5.1, 5.3). The number of new genera ("gen. nov."), new species referred to previously known genera ("sp. nov."), and taxa referred to previously recognized species ("recognized sp.") occurring in each unit of the CMF are shown in figure 5.3 and table 5.3. These combined rodent and ungulate data do not clearly indicate any trend in the "degree of endemism"

[9] One of these, *Colpodon antucoensis*, was previously described (Shockey *et al*., 2012).

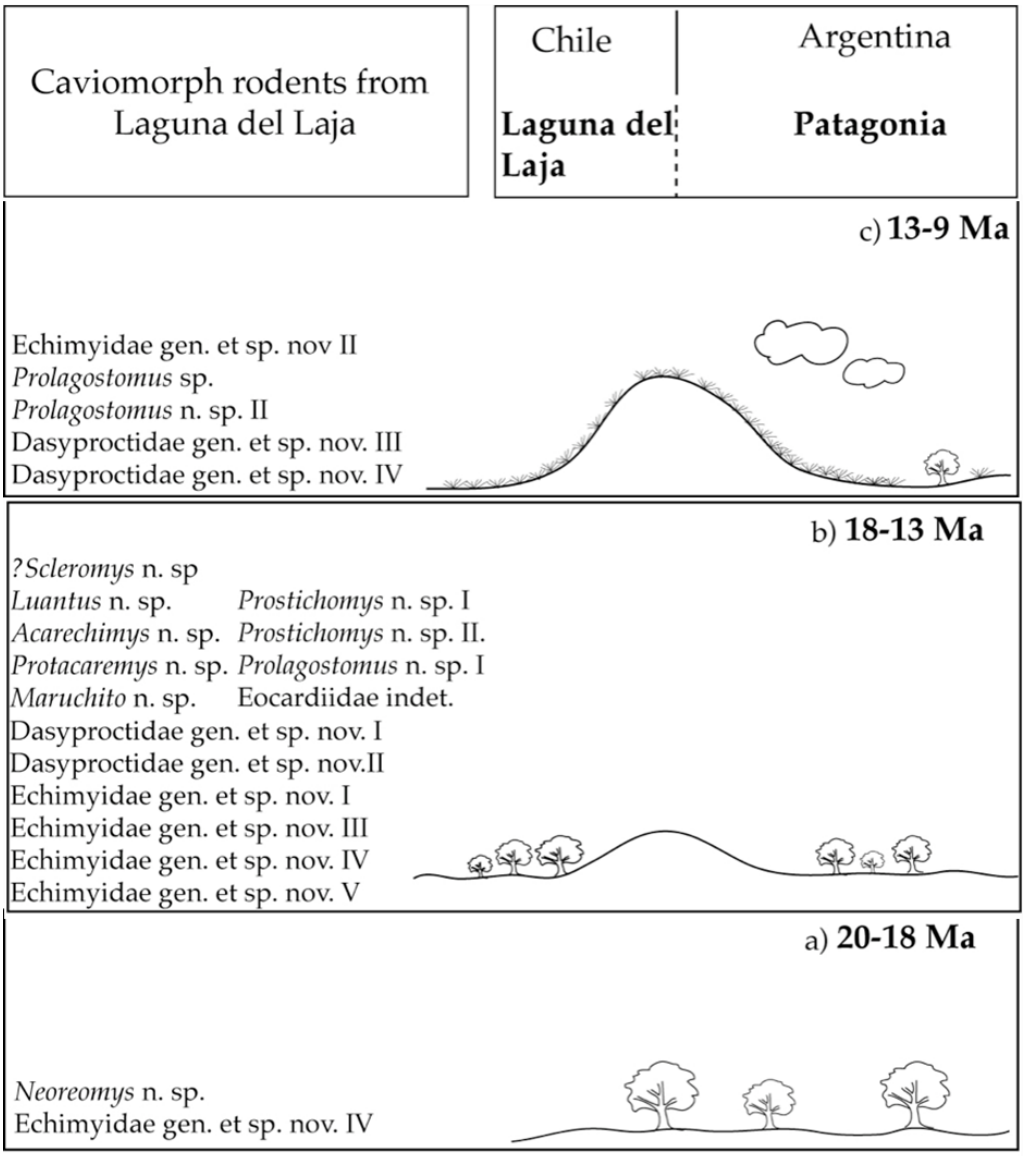


FIGURE 5.6. Schematic of the observed increase in endemism over time among rodent faunas from Laguna del Laja, and its hypothesized correlation with local uplift of the Andes cordillera. This illustration also highlights the possible transition (~13 Ma) from a closed forest environment to a cooler, dryer, grassland dominant environment, as indicated by increasingly hypsodont and hypselodont dentitions in rodents. From Wertheim, 2007.

TABLE 5.3. Endemism over time at Laguna del Laja.

Includes only taxa confidently identified to species-level. For taxa spanning more than one unit or subunit (*Protypotherium*, *Luantus*, Hegetotheriidae gen *et* sp. *nov*. A) only the first occurrence is indicated. See figs. 5.1 and 5.3 for stratigraphic relationships of each unit. See fig. 1.6 for descriptions of each unit. $Tcm_3$ is divided into two sections, the "lower beds" exposed at Estero Trapa Trapa East and the "upper beds" exposed at Estero Trapa Trapa West.

gen. nov. = newly described genera
sp. nov. = newly described species referred to previously recognized genera
recognized sp. = taxa referred to previously recognized species

| | Rodentia | Notoungulata and Astrapotheria | Rodents and Ungulates |
|---|---|---|---|
| $Tcm_5$ & $Ttt_1$ | 2 gen. nov. | | 2 gen. nov. |
| ~15 Ma | | | |
| $Tcm_4$ | 1 gen. nov.<br>1 sp. nov. | | 1 gen. nov.<br>1 sp. nov. |
| ~16 Ma | | | |
| $Tcm_3$ upper beds | 4 gen. nov.<br>3 sp. nov. | 1 gen. nov.<br>1 recognized sp. | 5 gen. nov.<br>2 sp. nov.<br>1 recognized sp. |
| ~17 Ma | | | |
| $Tcm_3$ lower beds | 2 gen. nov.<br>5 sp. nov. | 1 gen. nov. | 3 gen. nov.<br>5 sp. nov. |
| ~18 Ma | | | |
| $Tcm_1$ | 1 gen. nov.<br>1 sp. nov. | 3 gen. nov.*<br>1 sp. nov.<br>1 recognized sp. | 4 gen. nov.*<br>2 sp. nov.<br>1 recognized sp. |

*Includes Interatheriinae gen *et* sp. *nov*. C. The stratigraphic position of this taxon at Laguna del Laja is unknown, but at Las Leñas it is closely associated with an $^{40}Ar/^{39}Ar$ date of 20.09 ± 0.27 Ma (Flynn *et al.*, 1995).

across stratigraphic levels. Partially consistent with Wertheim's (2007) observations, more "sp. nov." than "gen. nov." occur from ~18-17 Ma, but the temporal intervals immediately preceding and succeeding this span exhibit nearly identical "degrees of endemism." No "recognized sp." are recorded at LdL after ~16 Ma, but, considering that these upper units include only four confidently identified species, this may simply reflect poor sampling.

Similarly, a qualitative assessment of typotherians from LdL is not consistent with a pattern of "increasing endemism" up the stratigraphic section. For example, Interatheriinae gen. *et* sp. *nov*. B (INT C) is the stratigraphically oldest taxon recovered from the CMF (see fig. 5.1), and yet it represents arguably the "most distinct" typotherian described in this study. INT C is diagnosed by several unusual characters, including a series of labial furrows on P4-M3, differences in "molarization" between P3/4, and the loss of one tooth without any other apparent dental reduction; each of these characters is unique among interatheriids (whereas most typotherians described in this study are diagnosed mainly by subtler differences and/or a unique combination of characters known among other taxa) (see Ch. 2).

An unambiguous pattern from LdL, clearly evident among *both* rodents and ungulates, is that the majority of taxa represent new species, and the majority of new species represent new genera (table 5.1). Since a high degree of endemism occurs throughout the CMF, it has little bearing on determining the timing of significant uplift in the region, but it does not exclude the possibility that Andean topography influenced the provinciality of the LdL faunas. During the Miocene, whether or not these mountains approached the elevation of the current cordillera, mammals in the LdL region lived in a volcanically active environment, subject to periodic ash falls and volcanic mudflows. In addition to providing at least some topographic barrier to dispersal, volcanoes would have likely provided unique and heterogeneous environments conducive to habitat fragmentation and geographically

isolated populations – conditions long thought to promote genetic divergence and speciation (e.g., Mayr, 1963; Lynch, 1989; Allmon, 1992). Endemism of the fossil mammals from LdL, in addition to highlighting the diversity of Miocene-aged South American mammals, also attest to the diversity of paleoenvironments in which they lived.

**High-crowned dentitions at Laguna del Laja**

Many groups of mammals have evolved high-crowned dentitions, but this pattern is especially striking in South America. High-crowned (hypsodont) dentitions have developed independently in perhaps 25 clades of South American mammals, half of which eventually developed open-rooted, ever growing (hypselodont) dentitions (Madden, 2014). Hypsodonty, considered to reflect abrasive diets (Damuth and Janis, 2011; Madden, 2014), is especially common among grazers that feed on phytolith-rich grasses in dry, gritty soils (Damuth and Janis, 2011). Accordingly, trends of increasing hypsodonty and hypseldonty in the fossils record are generally interpreted as reflecting the presence of relatively dry, grass-dominated paleoenvironments (e.g., Scott, 1913; Pascual and Odremán-Rivas, 1971; Verzi *et al.*, 1994; Pascual and Ortiz-Jaureguizar, 1990; Pascual *et al.*, 1996; Janis *et al*., 2002; Flynn *et al.*, 2003).

Rodents from LdL exhibit increasing crown height over time (Wertheim, 2007). Lower units of the CMF ($Tcm_{1-3}$) are dominated by echimyids with low-crowned dentitions, but higher in the stratigraphy ($Tcm_{4-5}$ and $Ttt_1$) hypsodont dasyproctids and hypselodont chinchillids become more common. This shift, though difficult to assign a precise age to at LdL, is roughly coincident with mid-Miocene global cooling that commenced at ~15 Ma (Zachos *et al*., 2001). Consistent with many previous interpretations of the origins of

hypsodonty, the increase in crown height among rodents from LdL, which occurs in-step with global cooling, suggests a possible shift towards a drier climate with open, grassland habitats (Wertheim, 2007) (see fig. 5.6). This interpretation is corroborated by the Patagonian pollen record, which indicates that grasses were present, but in low abundance, during the early Miocene, and became regionally dominant by the late Miocene (Barreda and Palazzesi, 2007; Palazzesi and Barreda, 2012).

Several recent studies, however, call into question the suggested link between hypsodonty and grasslands. The early Oligocene Tinguirirca fauna from the Andes of central Chile represents the oldest mammal assemblage in South America dominated by hypsodont herbivores (Flynn *et al*., 2003), but recent studies of pollen and phytolith records from Patagonia suggest that grass-dominated ecosystems were not established until after the early Miocene (Barreda and Palazzesi, 2007; Palazzesi and Barreda, 2012; Stromberg *et al*., 2013). Although regional differences are possible, it is difficult to imagine that grassland biomes appeared in central Chile more than 10 Ma before their proliferation in Patagonia. Moreover, recent dental microwear analyses of several early Miocene notoungulates with high-crowned dentitions suggest that, in some cases, taxa often interpreted as open-habitat grazers actually fed primarily on browse (Townsend and Croft, 2008). These results indicate that high-crowned dentitions are not necessarily linked to grasses, leading to various alternative proposals to account for the early prevalence of hypsodont and and hypselodont dentitions in South American mammals. Other potential sources of "abrasives" include different types of silica-rich plants (e.g., palms), dietary grit, and even volcanic ash and other pyroclastic particles (Pascual and Ortiz-Jaureguizar, 1990; Stromberg *et al*., 2013; Madden, 2014).

Post-Oligocene interatheriids and hegetotheriids, including the five new taxa described in this study, are characterized by hypselodont dentitions (fig. 5.7). Inasmuch as hypselodonty appeared in both these groups by the late Oligocene (fig. 5.7), the "degree of hypsodonty" of typotherians from LdL is moot with respect to the environmental shift inferred from rodent dentitions. The abundance of hypselodont typotherians in the lower units of the CMF at LdL (fig. 5.1, table 5.2), may signal the presence of dry, open environments by the early Miocene. After all, inferences about feeding behaviors, substrate uses, body sizes, and locomotor capabilities of Miocene typotherians generally suggest that they occupied open habitats, including savannahs, grasslands, and steppes (Cassini *et al*., 2012b). This interpretation, however, is admittedly tenuous, since typotherians (and other ungulates at LdL) did not all necessarily share identical habitats and feeding strategies. For example, *Interatherium* and astrapotheriids may have lived in close proximity to standing water (Cassini *et al*., 2012b), *Hegetotherium* possesses morphological characteristics common to mammalian woodpeckers (McCoy and Norris, 2012), and *Protypotherium* (well-represented at LdL) likely fed on browse (Townsend and Croft, 2008). These ambiguities concerning the feeding and habitat preferences of ungulates from LdL preclude firm paleoecological inferences. Consequently, the pattern of increasing crown height in rodents (Wertheim, 2007) may be more telling.

The record of hypselodont typotherians at LdL, while of limited paleoecological utility, is part of a fascinating evolutionary story. "Archaeohyracids" (paraphyletic outgroup to Hegetotheriidae) developed hypsodont dentitions near the Eocene-Oligocene Transition, and hegetotheriids attained fully hypselodont dentitions by the late Oligocene (fig. 5.7). A simultaneous but independent trend is seen among interatheriines (fig. 5.7). The Eocene-Oligocene Transition was marked by rapid and significant global cooling (Zachos *et al*.,

2001), suggesting a link between drier, cooler climates, changing paleoecological conditions, and the development of hypsodonty in "archaeohyracids" and interatheriids (among other groups[10]). Shifts in floral assemblages and possible changes in mammalian herbivore feeding behaviors over this interval remain poorly understood, but recent studies indicate that grasses did not become widespread in South America until the Miocene (Barreda and Palazzesi, 2007; Palazzesi and Barreda, 2012; Stromberg *et al*., 2013).

By the late Oligocene (Deseadan SALMA), interatheres and hegetotheres had developed hypselodont dentitions. Dental wear analyses indicate that many Deseadan typotherians were grazers with abrasive diets (though whether these abrasives originated from phytoliths or soil adhering to vegetation is uncertain) (Croft and Weinstein, 2008; Billet *et al*., 2009). Thus, the origin of hypseldonty in interatheriids and hegetotheriids is plausibly associated with grazing, even though recent evidence suggests that some later diverging, hypselodont typotherians were not grazers (e.g., Townsend and Croft, 2008; McCoy and Norris, 2012).

Although the diversity of hypselodont interatheriids and hegeotheriids in the Deseadan has long been recognized (e.g. Marshall and Cifelli, 1990; Reguero, 1999; Hitz *et al*. 2000, 2008; Reguero *et al*., 2003b; Madden, 2014), the current study highlights the degree to which these radiations were simultaneous, extensive, and likely linked to hypselodonty (fig. 5.7). A burst of diversification immediately followed the appearance of ever-growing cheek teeth (fig. 5.7). Hypselodonty was likely a key innovation sparking the spectacular success of hegetotheriids and interatheriids in the late Oligocene and Miocene, results of which include the five newly described typotherians from LdL.

[10] Hypsodont notohippids are also first recorded in the early Oligocene (Flynn *et al*., 2003).

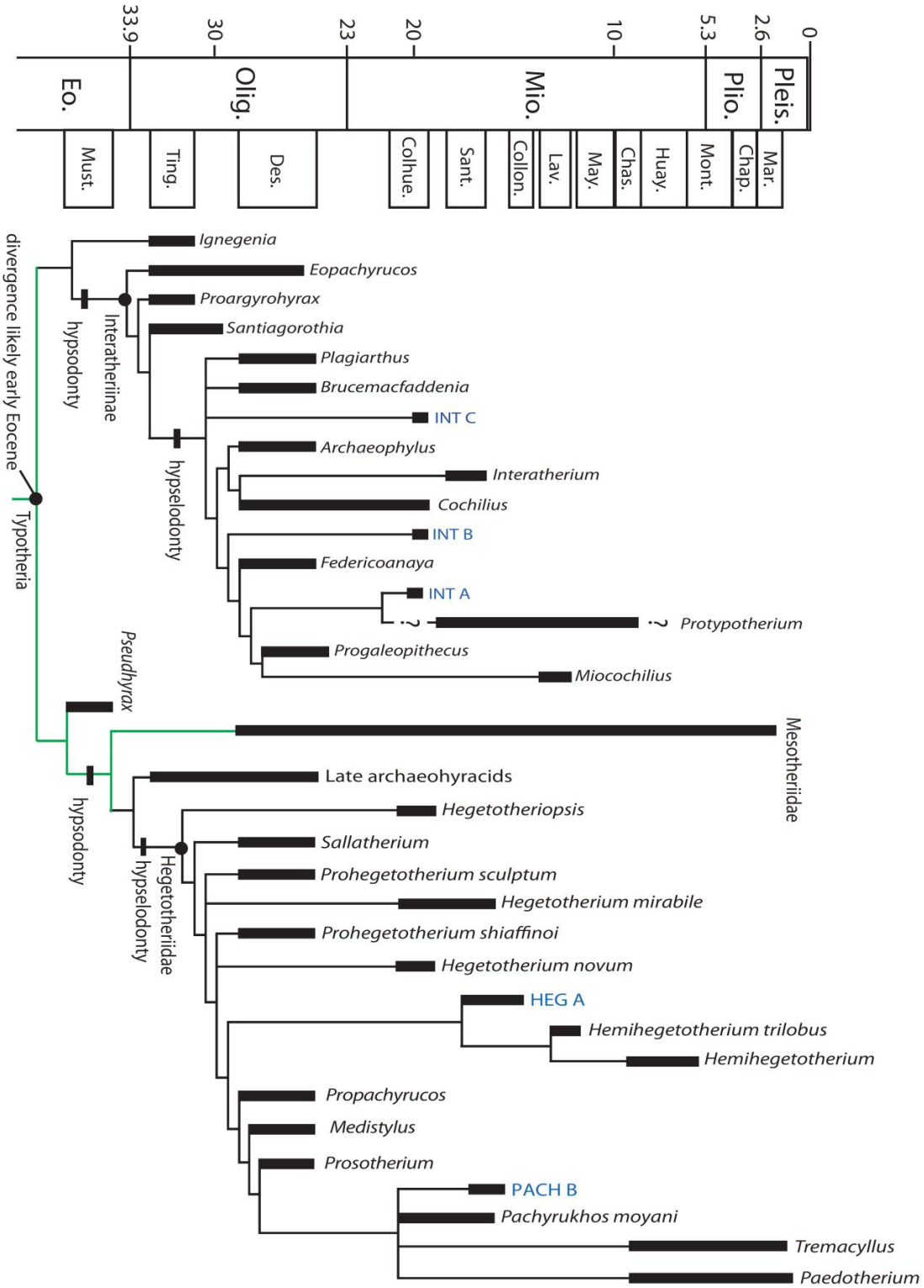


FIGURE 5.7. Phylogeny of Typotheria showing the stratigraphic position of included taxa (black bars). Relationships within Interatheriinae and Hegetotheriidae from the present study (Ch. 2 [see figs. 2.9, 2.10], and Ch. 3 [see figs. 3.8, 3.9]). Green portion of tree indicates relationships obtained from previous studies. Phylogenetic position of *Pseudhyrax* and Mesotheriidae following Billet *et al*., 2009. Ages for *Pseudhyrax*, Mesotheriidae, and divergence of Typotheria from Reguero and Prevosti, 2010.

# Conclusions

A minimum of six typotherian notoungulates and one astrapothere treated in this study advance our understanding of fossil mammal faunas from the LdL region. The stratigraphically thick, temporally long-ranging, and paleontologically significant volcaniclastic sequences of the CMF and TTF continue to produce exciting new insights. To date, 26 rodents and ungulates have been confidently identified at the species-level. Of these, 11 have been referred to previously recognized genera, all of which are also known from Miocene Patagonian localities. This suggests at least some degree of Patagonian faunal influence, with biostratigraphic ties especially evident during the "Pinturan" and Santacrucian SALMAs (but also present during the Colhuehuapian and Colloncuran SALMAs).

Considering these high-latitude faunal associations, and the proximity of several coeval Patagonian localities, the level of endemism of the LdL faunas is remarkable; 24 novel species have been identified, 15 of which are referred to new genera. Rodent faunas from LdL exhibit increased endemism at higher stratigraphic levels (Wertheim, 2007). This pattern has been interpreted as evidence for the timing of local uplift and the establishment of pronounced topographic barriers (Wertheim, 2007). Newly described ungulates provide additional sampling from intervals bearing few rodents, particularly low in the stratigraphic section. Collectively, notoungulates and rodents exhibit consistently high levels of endemism across the stratigraphic section, suggesting the presence of isolating topographic barriers at least as early as ~20 Ma (the age of the oldest fossils from LdL). Regional morphotectonic and geochronologic evidence constrains uplift of the Andes to between the late Eocene to the late Miocene (e.g., Jordan *et al*., 2001; Herriott, 2006; Mosolf, 2013), and

volcaniclastic sequences of CMF and TTF appear to have accumulated within an intra-montane basin (Herriott, 2006; Flynn *et al*., 2008). Thus, despite uncertainties about when significant uplift began, the mammals studied herein clearly inhabited a volcanically active region. This unusual paleoenvironment, conducive to habitat fragmentation and geographic isolation, may help account for the remarkable degree of endemism at LdL.

Rodents from LdL become increasingly hypsodont and hypselodont at higher stratigraphic levels (Wertheim, 2007). This increase in crown height over time may document a transition to drier and more open paleoenvironments (Wertheim, 2007), especially as this morphological change is roughly coincident with mid-Miocene global cooling (Zachos *et al*., 2001) and the progressive establishment of grass-dominated habitats in Patagonia (Barreda and Palazzesi, 2007; Palazzesi and Barreda, 2012; Stromberg *et al*., 2013). All typotherians from LdL are hypselodont, including those in the lowest units of the CMF. This exclusive hypselodonty, however, likely represents evolutionary inheritance rather than robust paleoecological insight. Hypsodonty developed convergently in interatheres and "archaeohyracids" (ancestors of hegetotheres) by the earliest Oligocene, possibly in response to changes in climate and ecology at the Eocene-Oligocene Transition. By the late Oligocene interatheres and hegetotheres had acquired hypselodont dentitions, leading to simultaneous and independent radiations within these clades; only hypselodont forms persisted into the Miocene. Though the initial development hypselodonty in these groups may reflect an adaptation to grazing (Croft and Weinstein, 2008; Billet *et al*., 2009), recent studies suggest that feeding and habitat preferences of Miocene typotherians varied (e.g., Townsend and Croft, 2008; Billet *et al*., 2009; Cassini *et al*., 2012b). Consequently, the exclusive hypselodonty of interatheres and hegetotheres from LdL provides limited insight into local changes in paleoecology during the Miocene. The pattern of increasing

crown height among rodents may be more paleoecologically informative, providing direction for future studies of the LdL faunas.

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